

Catalogue of the Antipatharia (black corals, phylum Cnidaria) collected by the IN2021_V04 and IN2022_V08 expeditions to the Australian Christmas Island and Cocos (Keeling) Islands Territories

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Abstract In this catalogue, 17 species belonging to 11 genera and 6 families of black corals (Anthozoa: Antipatharia) collected by the IN2021_V04 and IN2022_V08 expeditions to the Australian Christmas Island and Cocos (Keeling) Islands Territories are described and illustrated.

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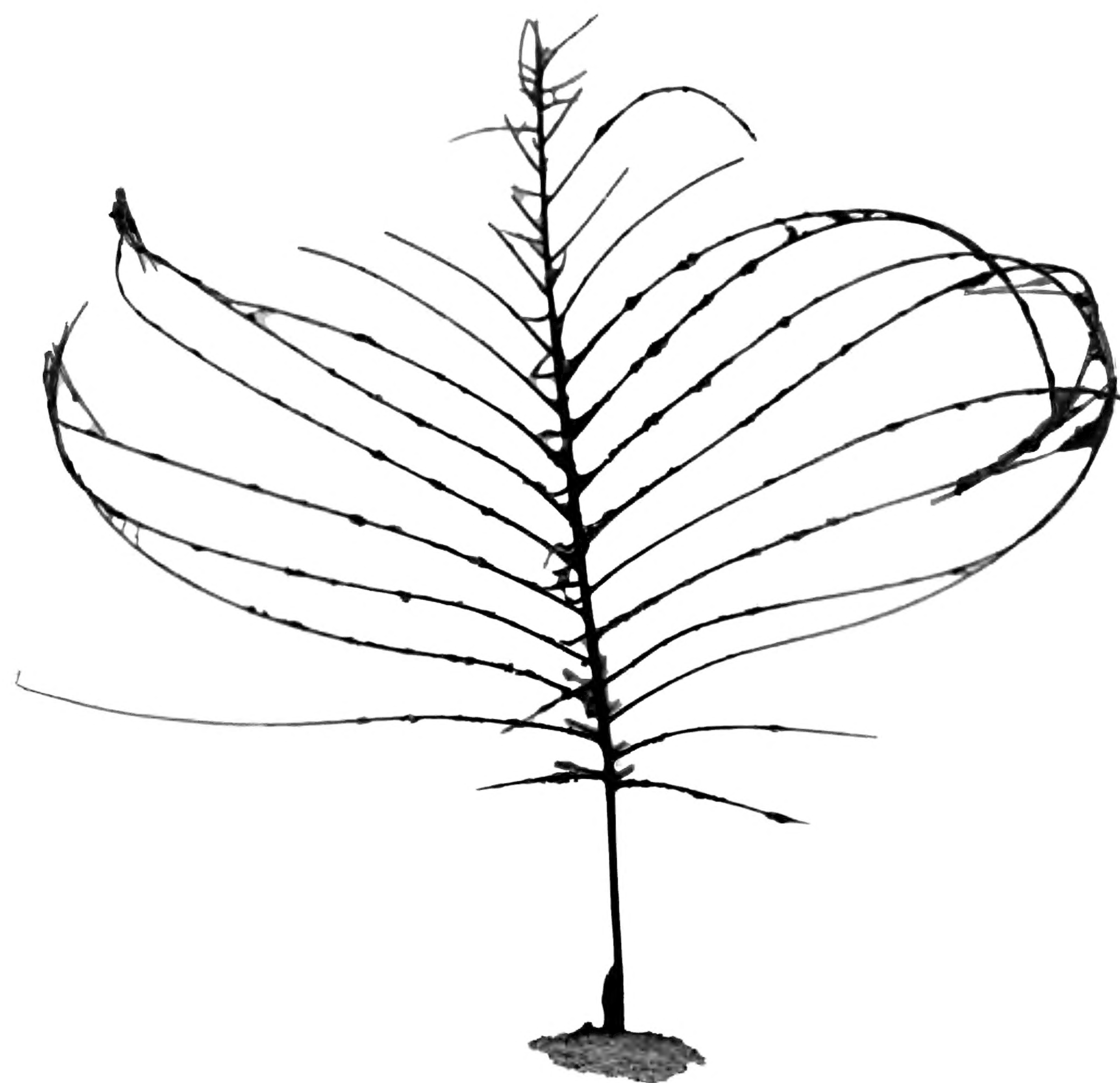


Figure 1. *Hexapathes bikofskii*.

Contents

Introduction	2
Methods	2
Systematic account	3
Family Antipathidae	3
Family Aphanipathidae	5
Family Cladopathidae	5
Family Leiopathidae	10
Family Myriopathidae	11
Family Schizopathidae	12
Acknowledgements	20
References	20
Species index	21
Species index	22
Appendix - Antipatharia from voyages IN2021_V04 and IN2022_V08 to the Australian Christmas Island and Cocos (Keeling) Islands Territories	23

Introduction

Black corals, an order of corals within the Hexacorallia, have historically been overlooked due to their habitat in deep waters and limited morphological features, which pose challenges for taxonomy. However, with the increase and advancement of deep-sea expeditions, there has been a surge in the collection and comparative analysis of black corals worldwide. This effort addresses fundamental gaps in biodiversity knowledge including elucidating differences between species and distribution patterns. Such knowledge is essential for implementing impactful conservation strategies.

This section catalogue presents the first comprehensive description of black corals from the deep Christmas and Coco’s (Keeling) Islands—Australia’s Indian Ocean Territories (IOT). It describes regional biodiversity, species-level range expansions, and sheds light on the ecological and evolutionary histories of this coral group. Specifically, it offers preliminary insights into reproductive mechanisms, substrate attachment, and relationships between species. Many hypotheses put forward in this catalogue necessitate further validation through the acquisition of additional specimens from neighbouring regions and the application of molecular techniques, preferably utilizing genome skim or ultra-conserved element analyses, on both IOT and global black coral collections.

Methods

Station details and collection methods are described in O’Hara (2024). Specimens from IN2021_V04 are stored in the collections of the Museum of Tropical Queensland, Townsville, Australia (MTQ) and specimens from IN2022_V08 are stored at Museums Victoria, Melbourne, Australia (NMV); see Appendix for details.

Three specimens collected in voyage IN2021_V04 (*Asteriopathes* sp. (Aphanipathidae), *Tylopathes* sp. (Stylopathidae) and *Trissopathes* cf. *tetracrada* (Cladopathidae)) are not included in the systematic account but are listed in the Appendix.

Systematic account

Family Antipathidae

Antipathes polyhedra Opresko, 2019

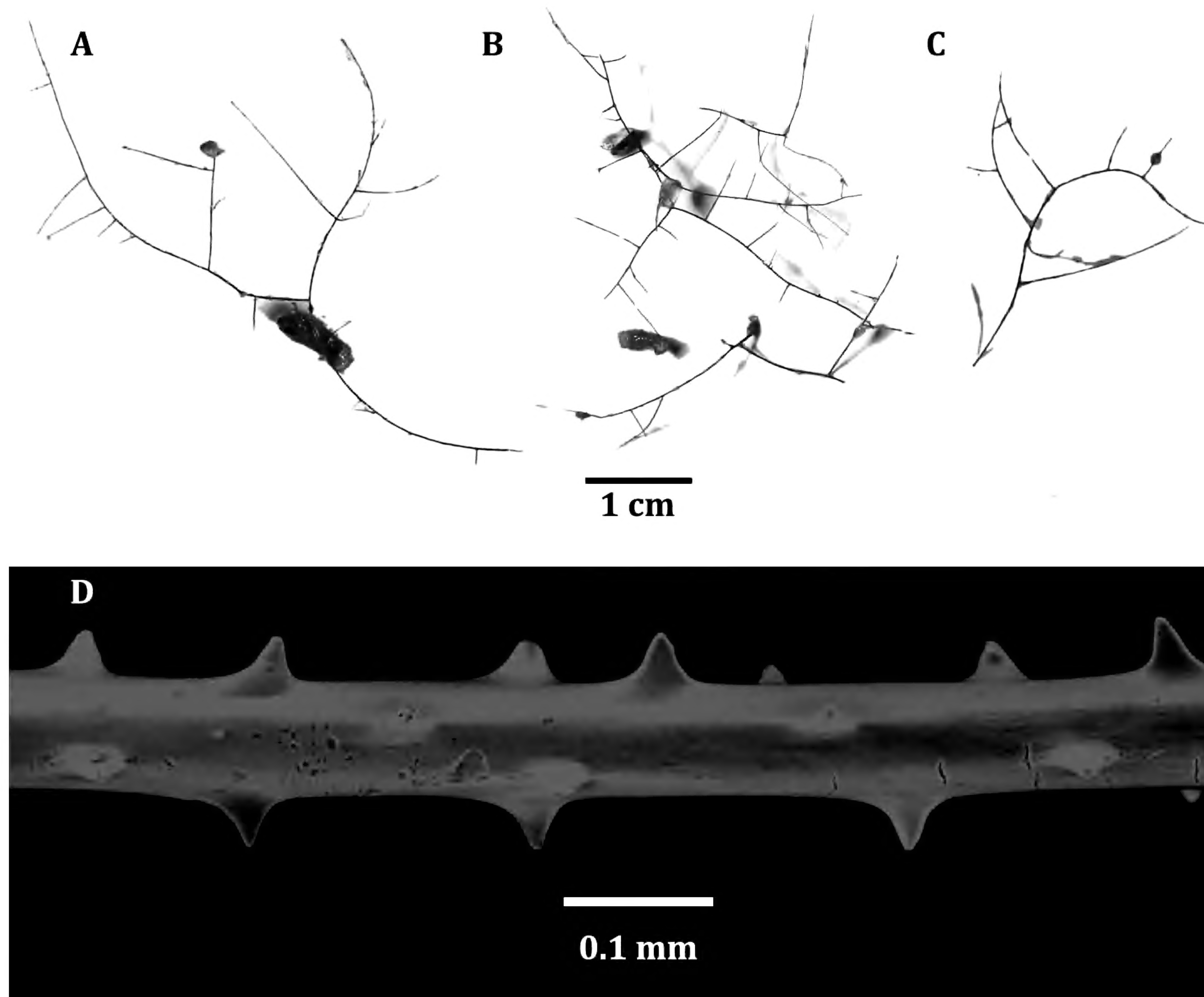


Figure 2. *Antipathes polyhedra*. (A-B) NMV F308495 (Op 179) multiple colonies dried. (C) NMV F308587 (Op 179) single colony dried. (D) NMV F308495 (Op 179) section of branch with spines.

Description of IOT material Colony 5 cm tall, sparsely branched to third or fourth order, planar, bramble-like coral with small holdfasts present at the tips of some branches. Secondary branches develop on all sides of lower order branches, with distal angles around 90° and lengths up to 5 cm. Spines narrow, smooth, arranged in four or five rows and 4-5 spines per mm in a row. Polypar spines 0.13 to 0.17 mm tall, abpolypar spines 0.07 to 0.1 mm tall.

Taxonomic remarks All specimens representing this species in previous and present studies have been collected via dredging. This is problematic because the act of dredging damages the specimens, confounding our knowledge of its morphological features, and tissue and DNA loss, limiting our ability to sequence and genetically compare this species to other nominal species. While currently placed in the genus *Antipathes*, this species occurs slightly deeper than its congeners and therefore could represent a novel genus because depth is thought to be a strong driver

of speciation for corals. It is recommended that specimens are collected via Remotely Operated Vehicle to determine habitat preference, describe in situ colony shape, and collect samples with intact tissue for genetic sequencing.

Distribution Kermadec Ridge, New Zealand (88–157 m); IOT (90 m).

Ecology and life history Little is known about black coral reproduction; however, during IN2022_V08 Op 179, 16 colonies representing *Antipathes polyhedra* were collected, suggesting either: they have a small range of dispersal, the species can reproduce asexually, or the location is highly suitable habitat for the species. Additionally, the presence of multiple holdfasts is rare for antipatharians, mainly found among bramble-like colonies found under overhangs. Given that this species has never been collected via remotely operated vehicle, it is unknown exactly how they attach to the substrate.

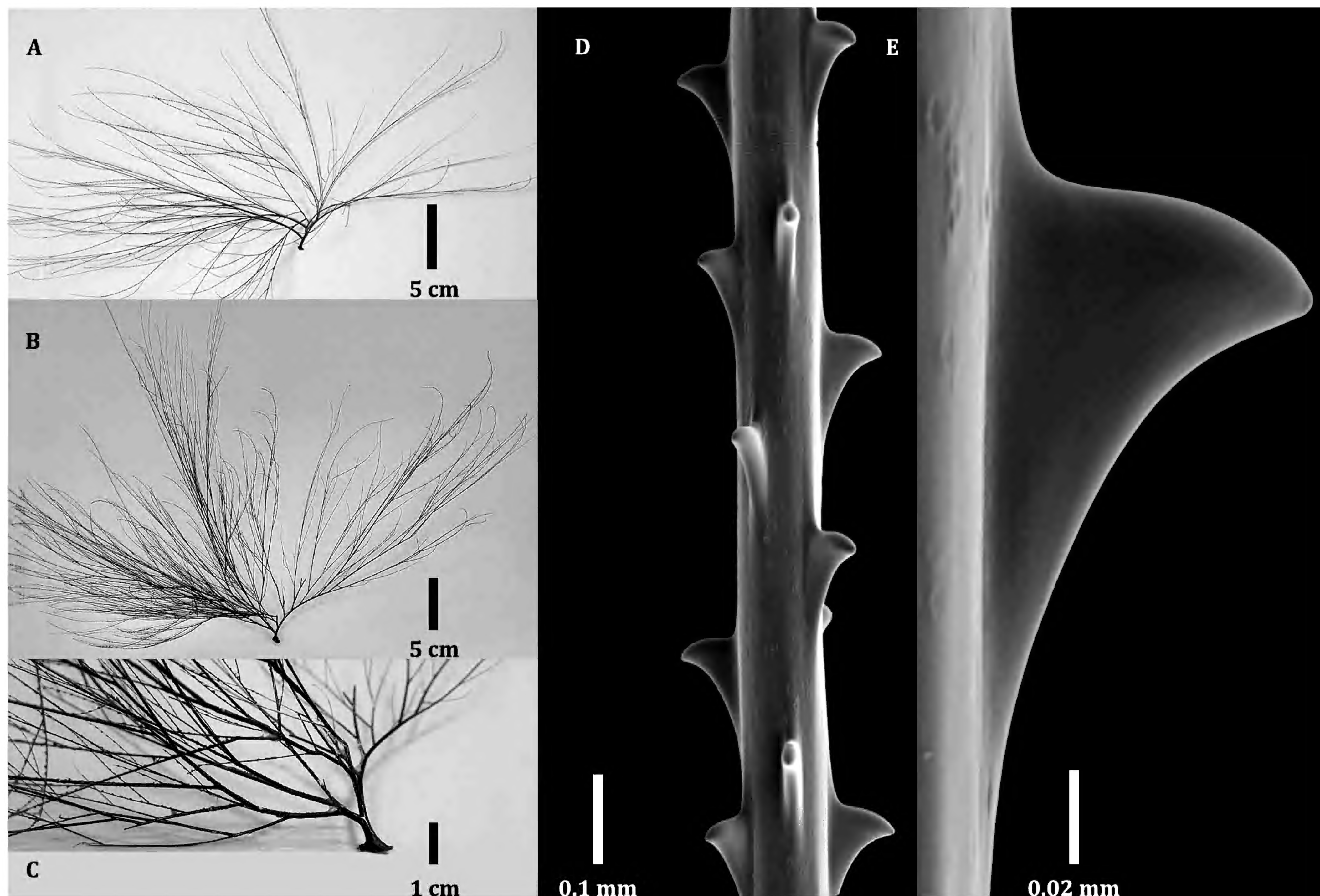
Antipathes aff. *leptocrada* Opresko, 2015

Figure 3. *Antipathes* aff. *leptocrada*. (A) NMV F308521 (Op 128) full colony dried. (B-C) NMV F308525 (Op 128) (B) full colony dried, (C) view of holdfast and lower stem. (D-E) NMV F308523 (Op 128) (D) section of stem showing spines, (E) single spine showing smooth surface and proximally-hooked tip.

Description of IOT material Colony upright, branched, planar about 30 cm tall. Flexible, elongate branches with narrow distal angles predominantly 30–50°. Branching to the fifth order, commencing 1 cm from the basal plate. Branches and branchlets are uniserial, emerging on the same side of lower order branches, spaced 1.5 to 2.5 cm apart in a single row. Terminal branchlets 24 cm or more in height. Spines are 0.08 mm tall, smooth, arranged in five axial rows, spaced 0.5 to 0.6 mm apart within each axial row. The distal edge of polypar spines extends to 0.1 mm in length, with the proximal edge reaching up to 0.16 mm. Polyps 1 to 1.5 mm in transverse diameter with 6 to 6.5 polyps per cm.

Taxonomic remarks The IOT specimen has many features like the type of *Antipathes leptocrada* including flexible, elongate branches, uniserial branches and branchlets emerging on the same side of lower order branches that are spaced 1.5 to 2.5 cm apart in a single row. Also like the type, the IOT specimen has spines that are 0.08 mm tall, smooth, and arranged in five axial rows, spaced 0.5 to 0.6 mm apart within each axial row. Lastly, the IOT specimen also has polypar spines with distal edges extending to 0.1 mm in length, with the proximal edge reaching up to 0.16 mm. However, The IOT specimen differs with regards to its much shorter terminal branches (4.5 cm vs 24

cm), more acute distal branch angle (20° vs 30 to 50°), fewer number of branching orders (3 to 4 vs 5), and being collected about 250 meters deeper than the currently known bathymetric extent of *A. leptocrada*. These differences, notably the much shorter terminal branchlet length, suggest it might be a species close to *A. leptocrada*. A more detailed morphological and genetic comparison is required to determine if the IOT specimen represents a new-to-science species.

Distribution Kermadec Ridge, northeast of New Zealand (88–157°); IOT (400 m).

Ecology and life history The spines of the IOT specimen and certain *Antipathes* species possess hooked-shaped spines suggesting some sort of specialized function; however, to date the function of black coral spines remains unknown. Function hypotheses include additional colony structure, and protection and support for polyps. Black corals have a wide range of spine types from being almost absent or lump-like in *Leiopathidae*, to forked or hooked in the *Antipathidae*, to highly ornamented with tubercles in the *Aphanipathidae*. This variation in spine morphology, with the oldest family, the *Leiopathidae* (Horowitz *et al.*, 2023b) having simpler spines, could indicate a trend towards increasing complexity in spine evolution across black corals.

Family Aphanipathidae

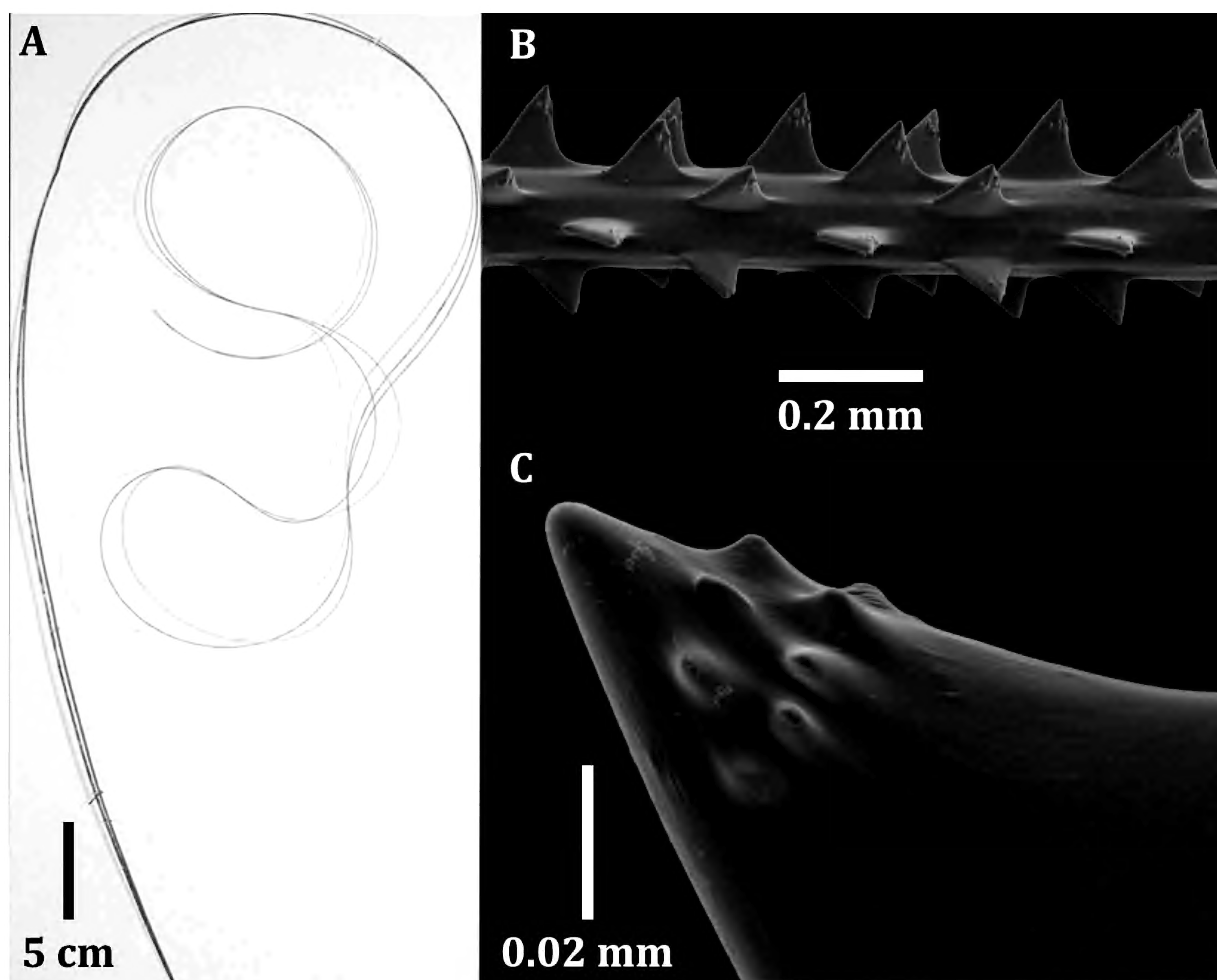
Aphanostichopathes sp. Bo & Opresko, 2021

Figure 4. *Aphanostichopathes* sp. (A-C) NMV F308527 (Op 161) (A) complete colony (B) section of skeleton with spines, (C) section of spine showing tubercles near spine tip.

Description of IOT material Colonies unbranched. Stem straight or curved and often forming wide distal coils. Spines usually conical, acute or blunt, with conical tubercles on their surface most often confined to near the apex. Polyps up to 3.4 mm in transverse diameter and arranged in a single series.

Taxonomic remarks *Aphanostichopathes* is a deep-sea (generally >1,000 m), and unbranched coral genus distinct from its unbranched shallow water (<1,000 m) counterparts (*Stichopathes*, *Cirripathes*, and *Pseudocirripathes*) due to former having conical tubercles on its spines. Species differentiation within this genus is based on spine tubercle characteristics, stem diameter, and polyp traits. The genus' cosmopolitan and bathymetric (down to the abyss) range extent suggests potential for more than the currently four nominal species. Notably, some specimens collected during the IOT expedition were from shallower depths (400 m) and possess fewer and less dense spine tubercles (Fig. 3C) compared to nominal species. Ten *Aphanostichopathes* specimens ranging from 400 to 5,000 m

depth were collected from IOT, necessitating detailed examination to determine which specimens represent new-to-science species and/or if *Aphanostichopathes* has bathymetric range extents shallower than 500 m depth.

Distribution Indian, Pacific, and Atlantic Oceans (1,000–5,000 m); IOT (400–5,000 m).

Ecology and life history The unbranched morphology was once thought to be a feature passed down from a common ancestor within the family, Antipathidae. However, molecular studies support the claim that unbranched black corals are found in two distinct families (Antipathidae and Aphanipathidae), and also that in both families, these genera are all polyphyletic (Horowitz *et al.*, 2023a). This example of convergent evolution suggests numerous independent evolutions of this simple non-branching character and is therefore an uninformative taxonomic character from species to family-level.

Family Cladopathidae

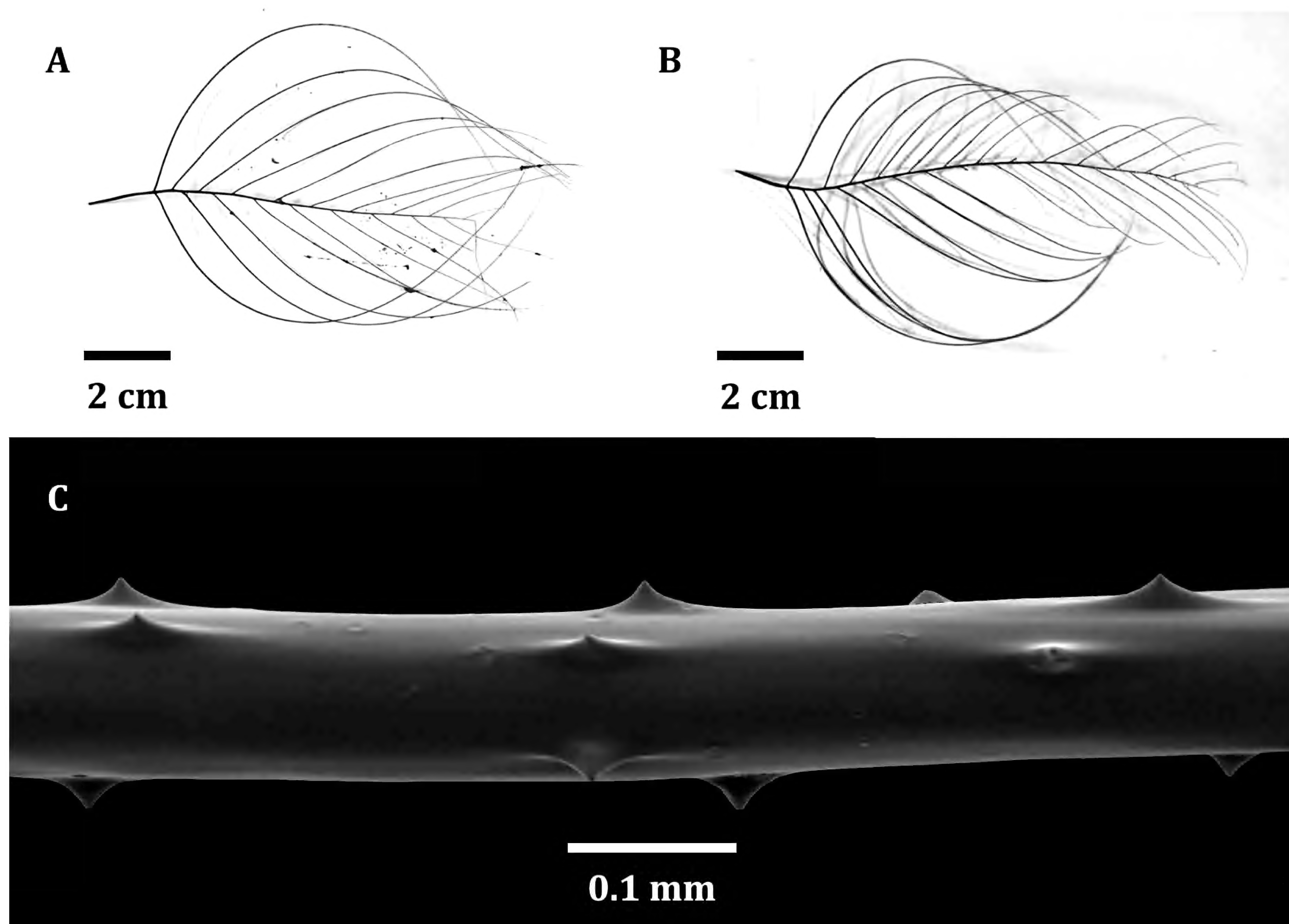
Abyssopathes anomalia Molodtsova & Opreskos, 2017

Figure 5. *Abyssopathes anomalia*. (A) NMV F308472 (Op 122) front view of full colony. (B) NMV F308489 (Op 183) front view of full colony. (C) NMV F308440 (Op 122) section of branch with spines.

Description of IOT material Corallum monopodial and pinnulate. Pinnules arranged in two lateral rows. Anterior pinnules usually absent. Lateral pinnules simple. Basal pinnules are generally not substantially curved in the posterior direction and, therefore, do not form a funnel-like structure. Spines on pinnules triangular, compressed, 0.02–0.03 mm long. Three to four rows of spines seen in lateral view; with three to six spines per millimeter in each row. Polyps up to about 5 mm in transverse diameter, with up to five polyps per 3 cm.

Taxonomic remarks Seven specimens collected during IOT have been identified as *Abyssopathes anomalia*, and 52 specimens have been identified as one of the nominal three species in *Abyssopathes*. The differences between species in the genus are slight, mainly being the presence and pinnulation of anterior pinnules. To date, no study has genetically confirmed that these are three distinct species. During IOT Op 122, 47 specimens representing all three species in the genus were collected, presenting an excellent opportunity to study boundaries between the three species in terms

of morphology and genetics

Distribution Central Pacific and Indian Oceans (5,025–5,130 m); IOT (4,000–5,000 m).

Ecology and life history The genus *Abyssopathes* exhibits remarkable morphological adaptations for surviving in the limited food resources of the deep sea. Unlike its shallower-water sister lineages, *Abyssopathes* spp. possess short, upward-growing stems that abruptly bend 90° to run horizontally. This prostrate habit is further enhanced by branches with a wind tunnel-like curvature. This adaptation maximizes food capture through two mechanisms. First, the horizontal stems and branches present a larger surface area perpendicular to the dominant flow direction, increasing encounter rates with potential food particles. Second, the wind tunnel shape channels water past the polyps, creating a low-pressure zone that actively draws nutrient-rich water into the polyps' mouths (Horowitz *et al.*, 2023a) This efficient system enables *Abyssopathes* to thrive in the food-scarce environment of the deep sea.

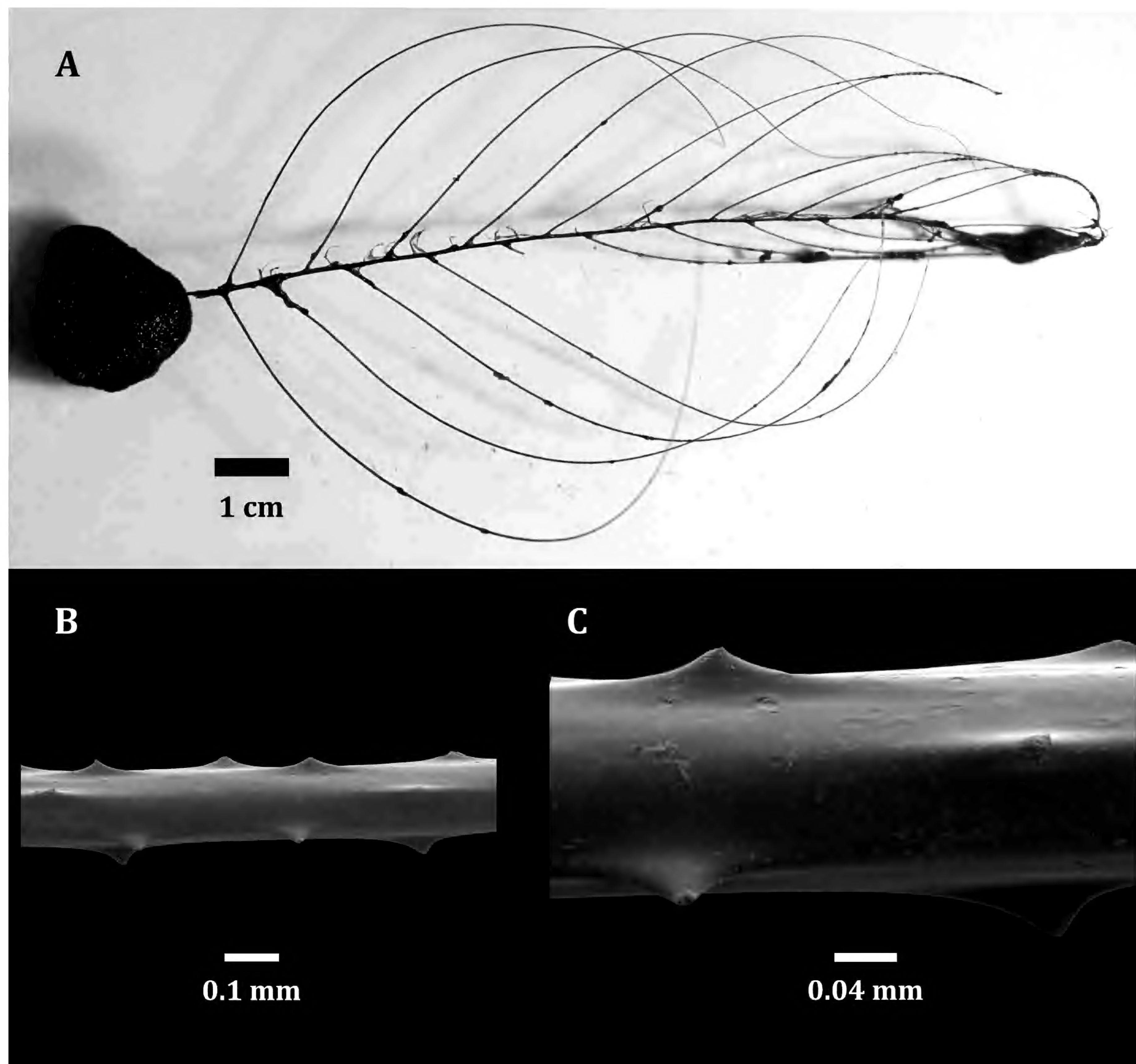
Abyssopathes lyra (Brook, 1889)

Figure 6. *Abyssopathes lyra*. (A-C) NMV F308599 (Op 122), (A) front view of full colony dried, (B-C) sections of stem showing spines.

Description of IOT material Corallum monopodial and pinnulate. Pinnules arranged in two lateral or anterolateral rows and one multiple anterior row. Lateral pinnules curved with distal ends of opposite rows meeting, forming funnel-like structure. Lateral pinnules simple, 8 counted per 3 cm. Anterior pinnules present simple, 7-10 counted per 3 cm. Spines on the lateral pinnules triangular, compressed, 0.02-0.04 mm long; those on anterior pinnules and subpinnules up to 0.03 mm long, and often inclined distally. Three to four rows of spines seen in lateral view with three to six spines per mm in a row. Polyps about 5 mm in transverse diameter; two polyps per cm.

Taxonomic remarks Twenty-eight specimens collected on IOT were identified as *Abyssopathes lyra*, representing one of the largest collections of the species collected from one location. As mentioned above, this collection presents an excellent opportunity to study morphological and molecular boundaries between species in the genus *Abyssopathes*.

Distribution Pacific, Atlantic, and Indian Oceans (3,459–3,492); IOT (4,000–5,000 m).

Ecology and life history IOT expedition Op 122 discovered the most extensive bed of *Abyssopathes* corals recorded to date, with a remarkable count of 53 specimens. Abyssal habitats are often characterized by possessing soft substrate like sand or mud (Horowitz *et al.*, 2023a); however, where these specimens were found, Cocos Abyssal, is an exception. The site features numerous small rocks, providing an ideal hard substrate for the settlement and development of these species. The unique presence of all three species in *Abyssopathes* in this location, flourishing in abundance, highlights the ecological significance of this rare abyssal habitat with suitable coral substrate. The discovery of this thriving *Abyssopathes* bed, consisting of three species, raises intriguing questions about the reproductive strategies of black corals. It suggests the possibility of shorter larval periods and limited dispersal distances in these species, contributing to the formation of densely populated coral beds such as this one.

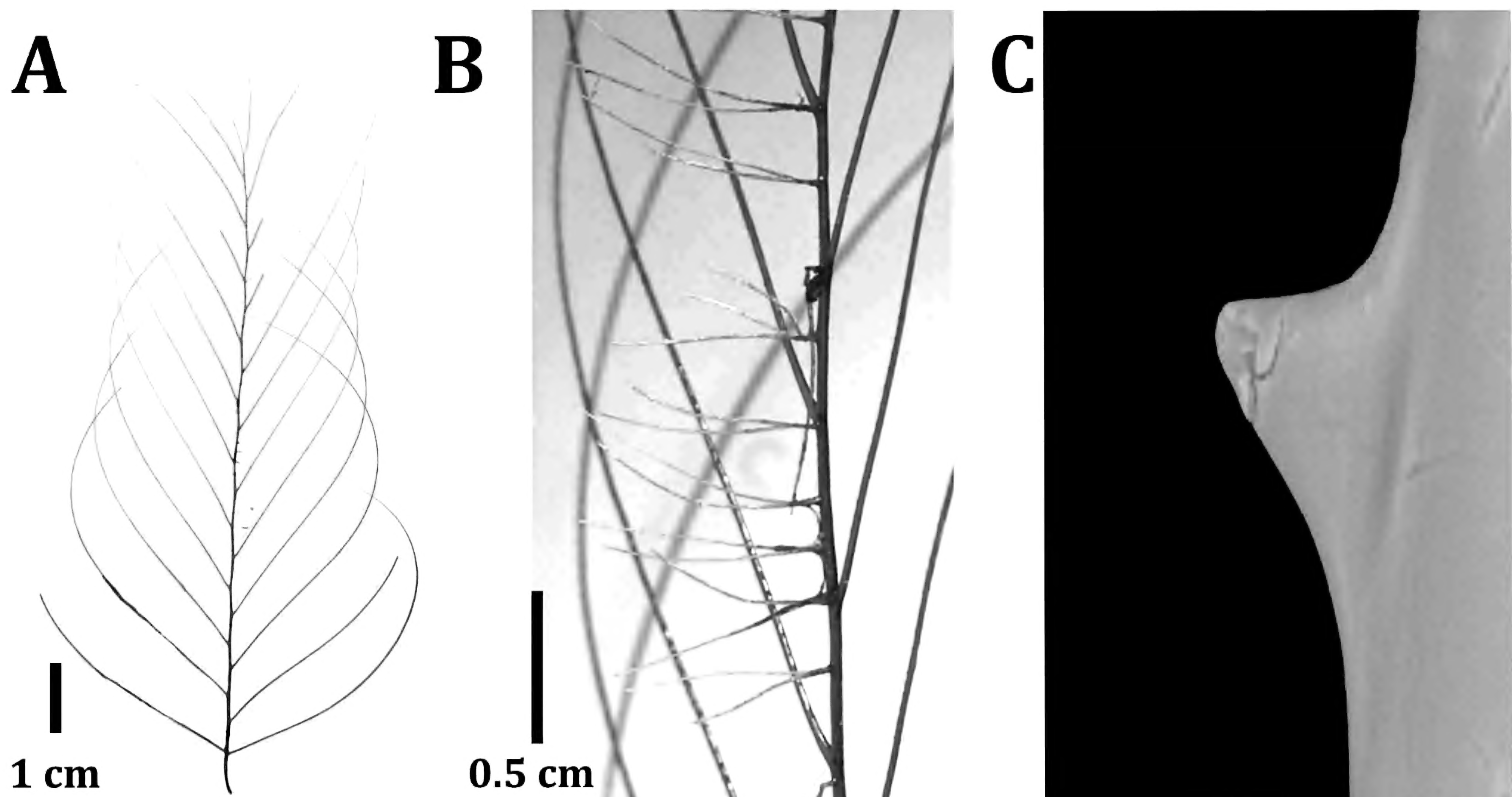
Abyssopathes lyraformis Opresko, 2002

Figure 7. *Abyssopathes lyraformis*. (A-C) NMVF308467 (Op 122), (A) front view of full colony dried, (B) Side view of stem showing subpinnulated anterior pinnules, (C) Section of skeleton showing a polypar spine (1.2k X magnification zoom).

Description of IOT material Corallum monopodial and pinnulate. Pinnules arranged in two lateral or anterolateral rows and one multiple anterior row containing two to three times the number of pinnules in either lateral row. Lateral pinnules simple; anterior pinnules usually with one, rarely two, secondary pinnules. Tertiary pinnules very rarely present on some secondary pinnules. Spines on the lateral pinnules triangular, compressed, 0.02-0.04 mm long; those on anterior pinnules and subpinnules up to 0.06 mm long, and often inclined distally. Three to four rows of spines seen in lateral view; with three to eleven spines per millimeter in each row. Polyps unknown.

Taxonomic remarks Sixteen specimens collected on IOT were identified as *Abyssopathes lyriformis*. As mentioned above, this collection presents an excellent opportunity to study morphological and molecular boundaries between species in the genus *Abyssopathes*.

Distribution Central Pacific, Atlantic, and sub-Antarctic (3,100–4,892 m); IOT (5,000 m).

Ecology and life history The three *Abyssopathes* species, found in deep habitats of multiple ocean basins but no one species being cosmopolitan, show a balance of wide dispersal and local adaptation, indicating varied dispersal strategies and life history traits suitable for different deep-sea conditions. Their wide but non-cosmopolitan range is important for conservation, highlighting the need to account for both broad oceanographic processes and local habitats, and offers insights into responses to global changes like climate change. A site with all three *Abyssopathes* species in abundance suggests a unique evolutionary site, revealing significant genetic diversity in the abyss and suitable hard substrate. This indicates a healthy, balanced ecosystem, with implications for conservation, especially if species are endemic or threatened. The site's condition could reflect environmental health and provides a valuable opportunity for research and ecological monitoring.

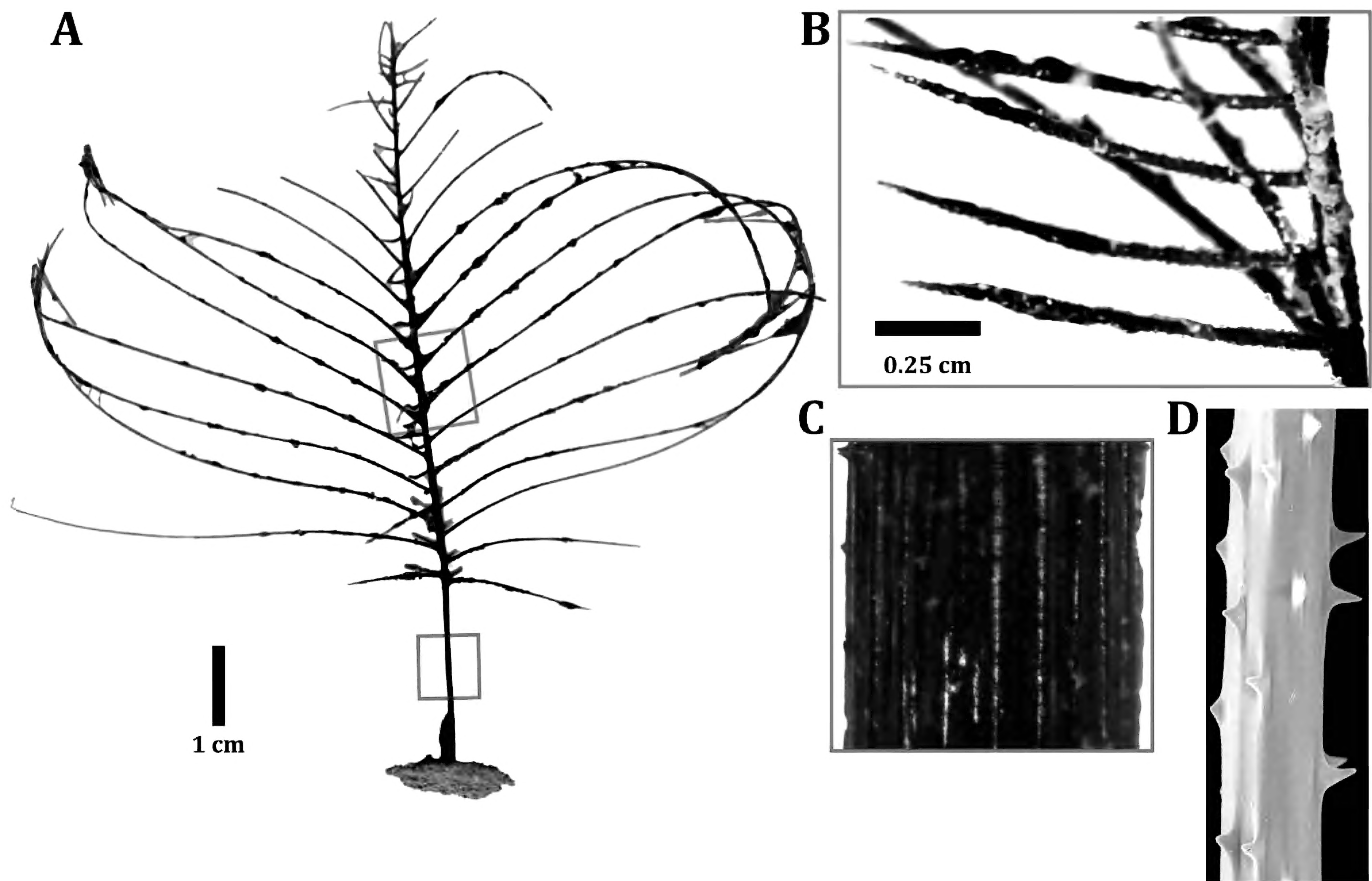
Hexapathes bikofskii Horowitz, 2022

Figure 8. *Hexapathes bikofskii*. (A-C) NMV F308503 (Op 163) (A) full colony dried, (B) zoomed-in side view of anterior pinnule with location where image was taken depicted by orange box, (C) zoomed-in view of unpinnulated section of stem showing striatum with location where image was taken depicted by blue box, (D) section of anterior pinnule showing skeletal spines (120 X magnification zoom).

Description of IOT material Colony monopodial, unbranched, and pinnulate. Pinnules arranged in two lateral rows and one anterior row. Basal-most pair of lateral pinnules subopposite, other lateral pinnules alternating. Striatum present from 1 cm above basal plate to first anterior pinnules. Lateral pinnules simple, up to 12 cm long, densities of six to 10 per 3 cm counting both rows. Anterior pinnules simple, 0.8 to 1.2 cm in length, densities of 11 to 15 per 3 cm. Polyps 4 to 6 mm in transverse diameter.

Taxonomic remarks The IOT expedition was the first to collect *Hexapathes bikofskii* from outside its type locality of eastern Australia (Horowitz *et al.*, 2022). Being collected west of Australia reveals that the species has a larger range than previously thought. *Hexapathes* contains species that occur at depths too deep for SCUBA and close circuit rebreather divers (greater than 400 m depth), and often shallower than common exploration depths with remotely operated vehicles (less than 1,000 m depth). This under-explored depth

range seems to represent great hidden diversity and more exploration at these depths will lead to a better understanding of biodiversity and species' range extents.

Distribution Great Barrier Reef and Coral Sea, Australia (638–789 m); IOT (510 m).

Ecology and life history The paratype of this species was collected attached to a nautilus shell (Horowitz *et al.*, 2022). This unique ecological interaction is often highlighted in discussions with the intriguing phrase, "a relict species was found growing on a relict species." This phrase encapsulates the remarkable encounter of two ancient, enduring forms of life, each with a deep evolutionary history, intersecting in a rare and insightful moment. This discovery not only offers a glimpse into the resilience and adaptability of these species but also underscores the complexity and interconnectedness of marine ecosystems.

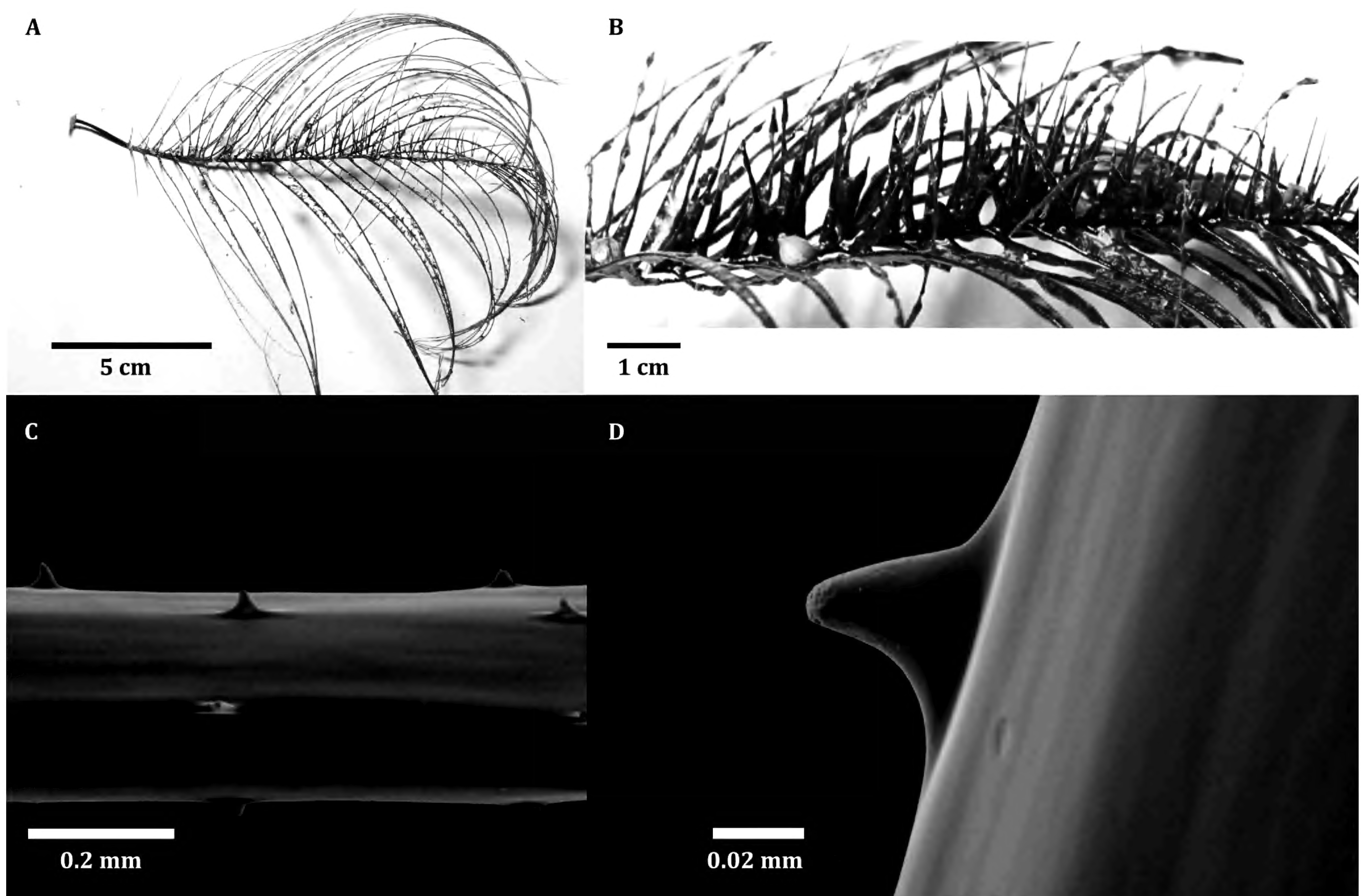
Hexapathes sp. Kinoshita, 1910

Figure 9. *Hexapathes* sp. (A-D) NMV F308504 (Op 163). (A) front view of full colony. (B) side view of full colony. (C) section of lateral pinnule with spines. (D) section of lateral pinnule showing spine.

Description of IOT material Corallum monopodial and pinnulate. Primary pinnules in two lateral rows and in one or more irregular anterior rows. Lateral pinnules simple, elongated, arranged alternately except for the most basal ones that are subopposite; inclined distally with curved distal part. Anterior pinnules simple or with one or two secondary pinnules, of varying length, always shorter than lateral pinnules, inclined distally, more densely set than lateral ones. Spines on pinnules small, triangular to conical in lateral view, smooth, 0.03-0.09 mm tall, mostly 0.04-0.07 mm, arranged in irregular axial rows, five to seven of which are visible in side view. Polyps estimated to be 2.5-6 mm in transverse diameter.

Taxonomic remarks There are taxonomic questions surrounding the relationships between species within the genus *Hexapathes* because of the slight morphological differences between species that might be related to the age of the colony. One of the main morphological distinctions between species is to what

extent, if any, are the anterior pinnules branched. It is possible that anterior pinnules start out short, simple, and become taller and more pinnulated with age. Therefore, more specimens representing simple and complex morphologies of each of the five species in the genus should be sequenced and compared morphologically.

Distribution Between 66° N and 66° S in Atlantic, Pacific, and Indian Oceans (400–900 m); IOT (510 m).

Ecology and life history Very little is understood about how black corals reproduce, especially among deep-sea species. However, some species in this family, Cladopathidae, hold their eggs at the base of densely populated anterior pinnules, suggesting these polyps and branches are specialized for reproductive purposes. Scientists have yet to study how the skeletal structure is different in these specialized regions of the colony, which could lead to a better understanding of how they reproduce.

Family Leiopathidae

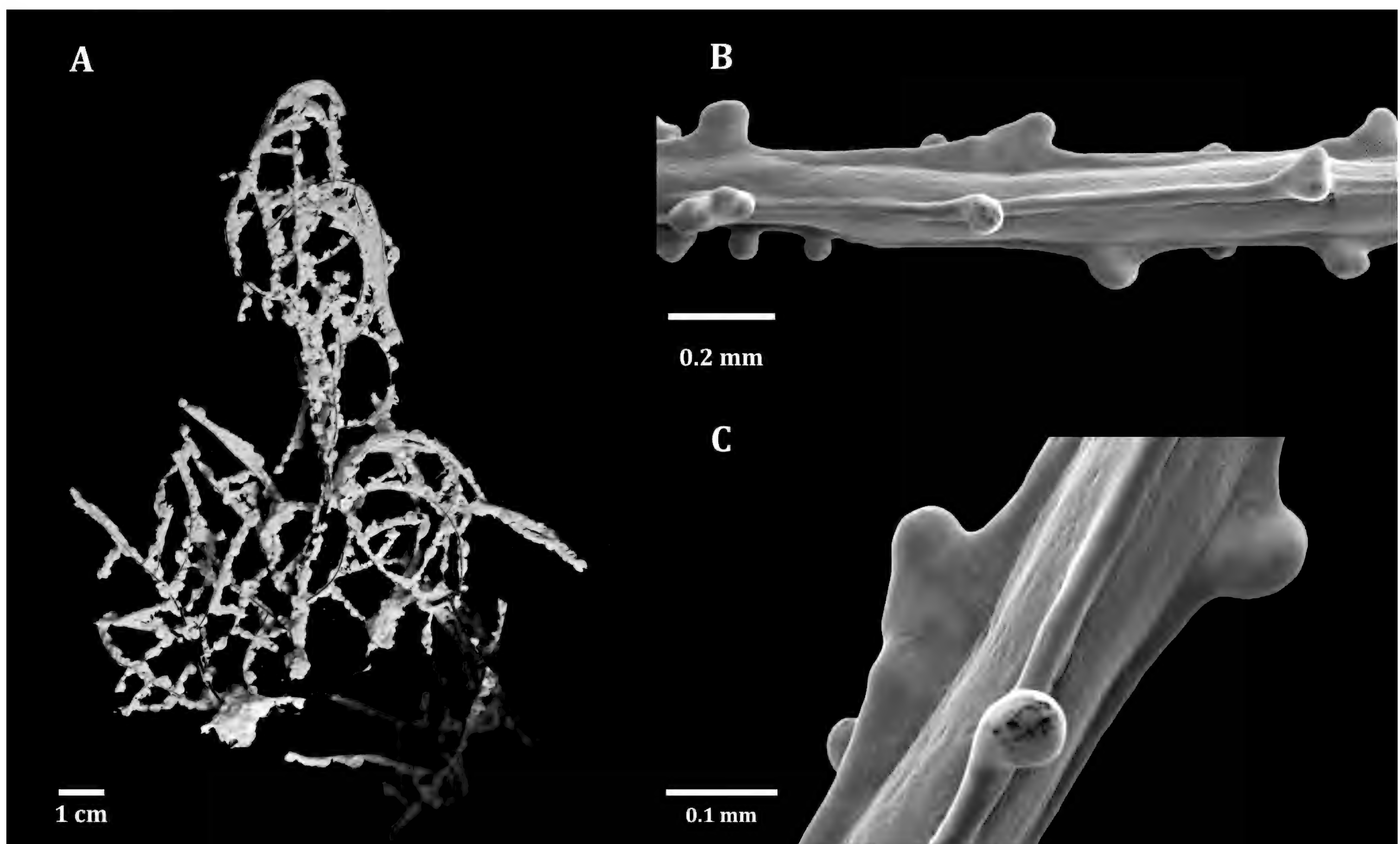
Leiopathes sp. Haime, 1849

Figure 10. *Leiopathes* sp. (A-C) NMV F308499 (Op 128). (A) complete collected fragment. (B) section of branch showing spines. (C) zoomed-in section of branch showing spines.

Description of IOT material Corallum irregularly sympodially branched but not pinnulate; branching multidirectional or flabellate. Branchlets arranged irregularly, loosely bilateral or uniserial, usually bent to some degree. Spines small, simple with smooth surface; triangular, conical or blister-shaped, often poorly developed or absent on older parts of the corallum. Polyps with 12 mesenteries; round with well developed tentacles, arranged in a single row at terminal branchlets. Adjacent polyps often unequal.

Taxonomic remarks The monotypic family Leiopathidae consists of just 10 species. Intra-species variation in branching characteristics and under-developed or absent spine features, makes differentiating species difficult. Most species have yet to be sequenced, high-

lighting a high priority area of future research.

Distribution Between 66° N and 66° S in Atlantic, Pacific, and Indian Oceans (300–2,000 m); IOT (350–400 m).

Ecology and life history Leiopathidae is the oldest family in the order, dated to over 400 million years old, which is about twice as old as most black coral families (Horowitz *et al.*, 2023b). Additionally, individual specimens can live over 4,000 years old, representing one of the longest-lived corals in the world (Brugler *et al.*, 2013). It isn't known how they have persisted for so long and how individual colonies can avoid cancer for so many years. Answers could provide insight into cures for cancer.

Family Myriopathidae

Myriopathes sp. Opresko, 2001

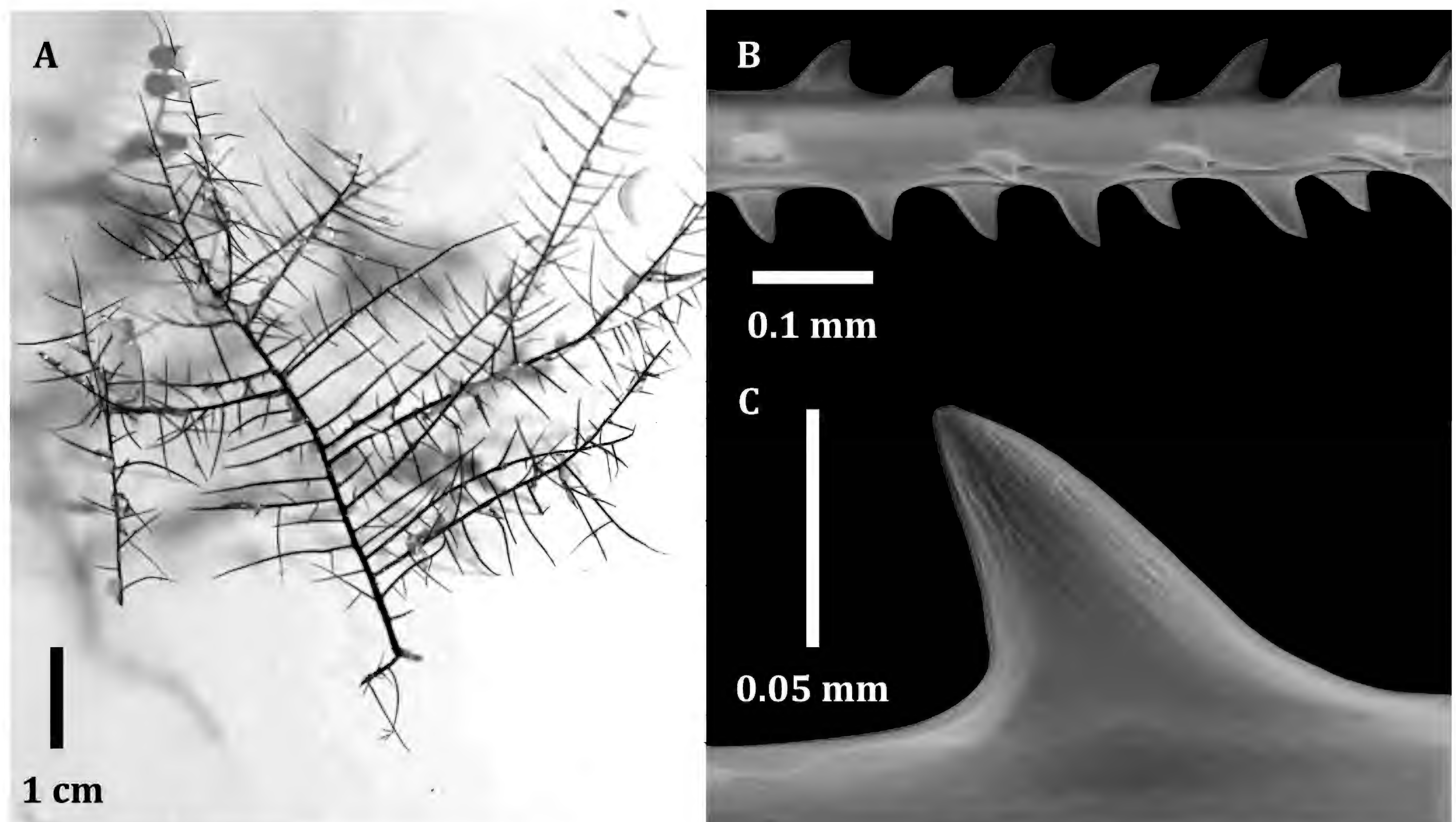


Figure 11. *Myriopathes* sp. (A-C) NMV F308493 (Op 138) (A) full colony. (B) section of pinnule with spines. (C) spine showing faint striations.

Description of IOT material Corallum flabellate or bushy. Stem and branches pinnulate to second order or more. Primary pinnules arranged bilaterally and alternately in two lateral or anterolateral rows. Secondary pinnules uniserially at base of primary pinnules, becoming biserial distally. Uniserial secondary pinnules usually projecting out of plane formed by biserial primary pinnules. When present, tertiary pinnules develop on secondary pinnules closest to base of primary pinnule.

Taxonomic remarks This IOT specimen presents a taxonomic puzzle. While its morphology aligns with *Myriopathes* and the family Myriopathidae in some aspects - flabellate shape, pinnules branching to the second or third order, and striations on skeletal spines - other features suggest a different family. The most significant discrepancies are the pinnule angles and depth of collection. Myriopathid pinnules typically

have much smaller distal angles (30-45°) compared to the specimen's 90° angles. Additionally, Myriopathidae species are not found at such depths - the IOT specimen was collected at 700 m, far deeper than their usual range.

Distribution Indian, Pacific, Atlantic, and Antarctic Oceans (10-70 m); IOT (700 m).

Ecology and life history Two explanations exist for this unusual Myriopathid-like specimen at 700 m depth. One possibility is that it originated from shallower waters and detached from its substrate, sinking to 700 meters. The other, more intriguing explanation considers both the unique pinnule angles and the collection depth. It suggests this specimen might represent an entirely new family. However, confirming its identity as a known species or a novel one requires genetic analysis.

Family Schizopathidae

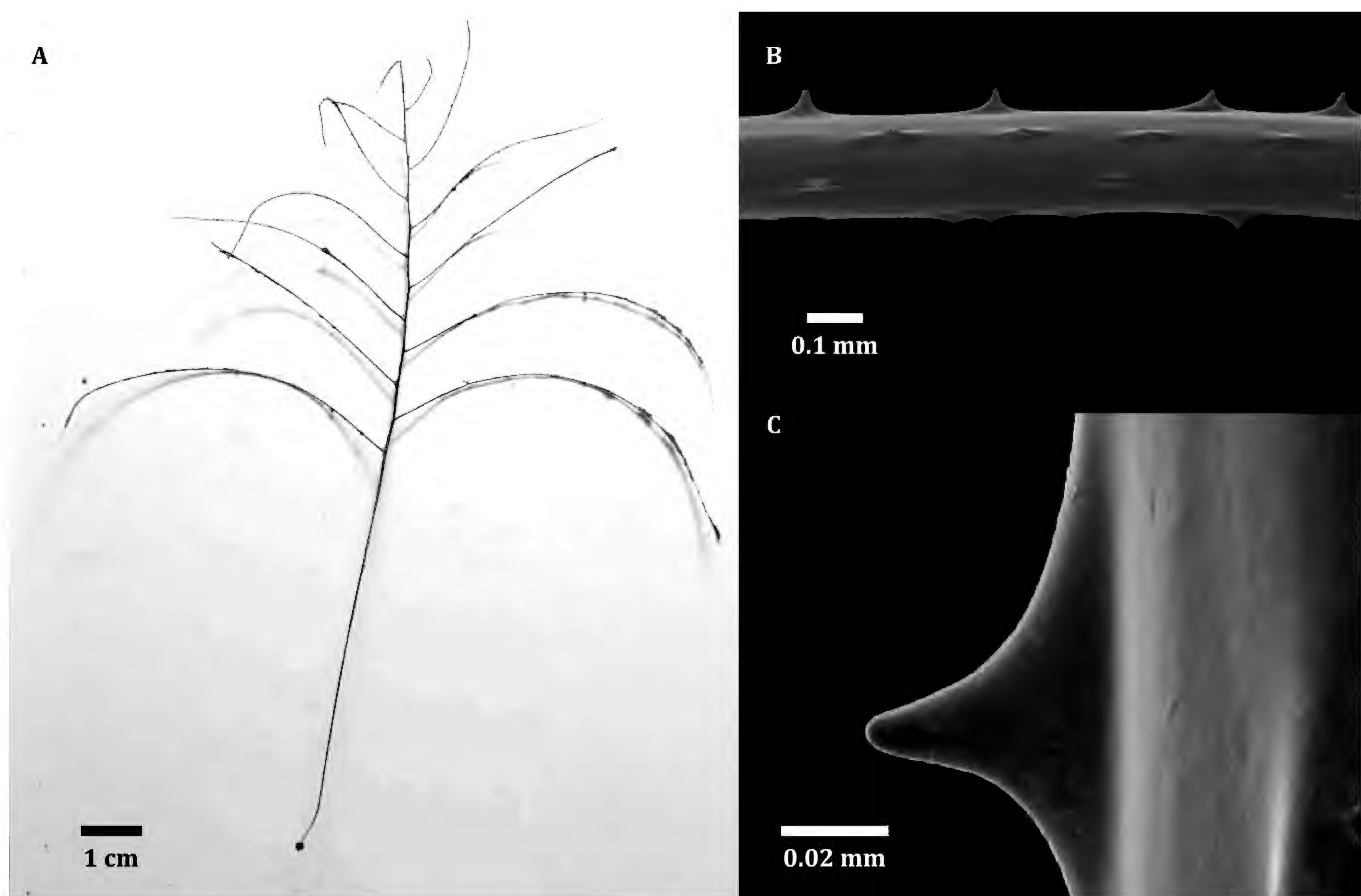
Alternatipathes alternata (Brook, 1889)

Figure 12. *Alternatipathes alternata*. (A-C) NMV F308481 (Op 122). (A) complete collected fragment. (B) section of skeleton showing spines. (C) Section of spine.

Description of IOT material Corallum attached to substrate; monopodial, unbranched or branched, and pinnulate. When present, pinnate branches of the first, second, and rarely third order arise from lowermost pinnules of stem. Pinnules simple, arranged alternately (including lowermost pair) in two lateral rows. Length of pinnules decreasing regularly from lower pinnulated section of stem to apex, forming a somewhat triangular outline. Striatum absent. Spines conical, smooth, simple (or rarely forked), with acute to slightly rounded apex and flared base. Spines larger on polypar side of pinnule. Size of spines apparently increases in older colonies. Polyps 2–4 mm in transverse diameter; arranged in one row with up to three

polyps per centimeter.

Taxonomic remarks *Alternatipathes*, *Umbellapathes*, and *Schizopathes* each have alternating pinnules, and the differences between these genera are the absence of a distinct basal plate (*Schizopathes*), absence of secondary pinnules (*Alternatipathes*), and presence of secondary pinnules (*Umbellapathes*). Therefore, robust molecular comparisons of all species in these genera are required to conduct a review of the Schizopathidae and revise these genera.

Distribution Indian, Pacific, Atlantic, and Antarctic Oceans (2,670–5,089 m); IOT (5,000 m).

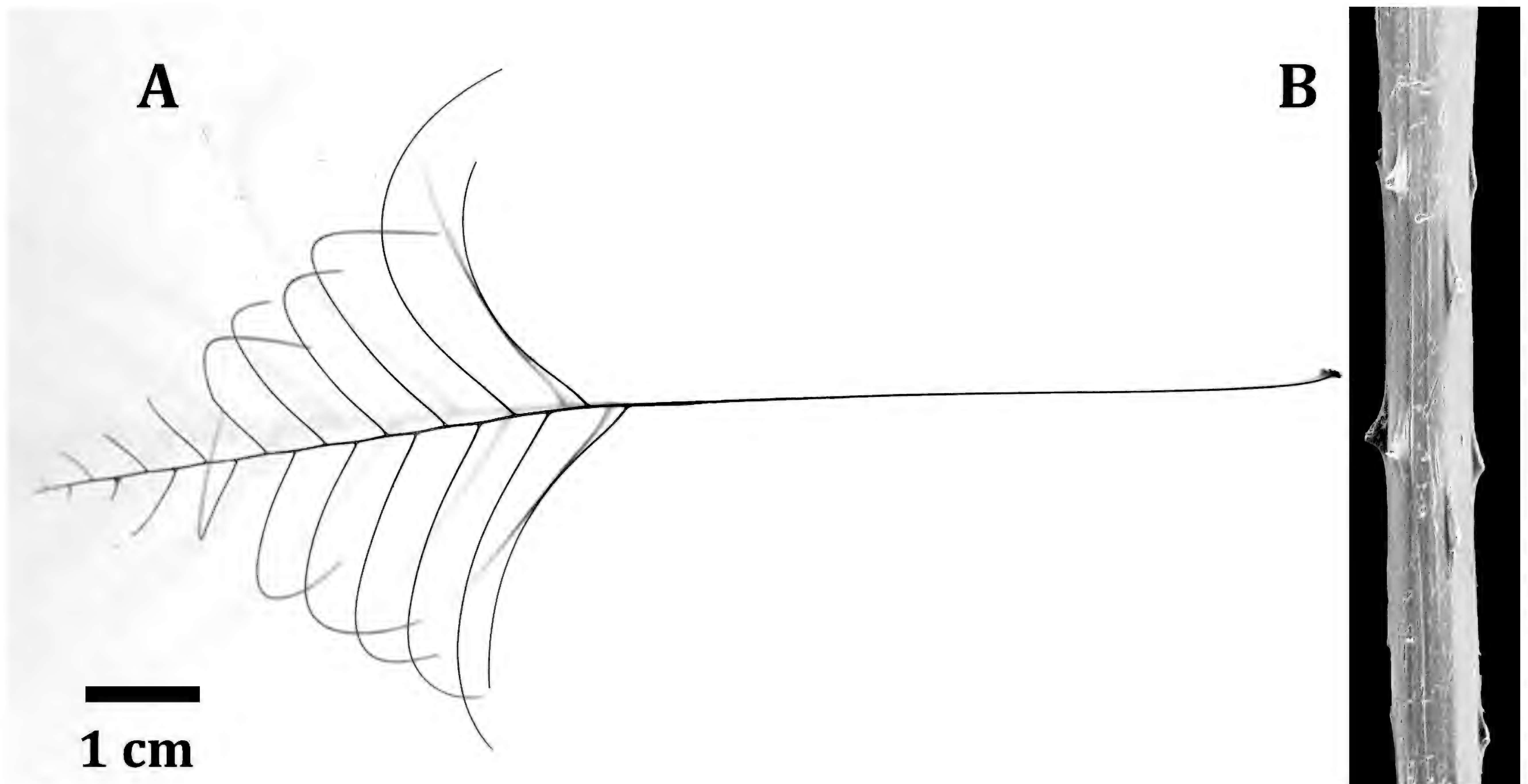
Alternatipathes maribilis Opresko & Molodtsova, 2021

Figure 13. *Alternatipathes maribilis*. (A–B) NMV F308484 (Op 120). (A) Complete collected fragment. (B) Section of pinnule showing skeletal spines (100X magnification zoom).

Description of IOT material Colony attached, monopodial, unbranched, and pinnulate. Pinnules simple, arranged alternately in two lateral rows along upper part of stem. Lower unpinnulated section of the stem longer than upper pinnulated section. Pinnules generally decreasing in length proximally to distally. Pinnular density 10–11 per 3 cm (including pinnules in both rows). Spines on pinnules smooth, triangular in profile, moderately acute, laterally compressed, and mostly 0.04–0.06 mm tall on polypar side of axis. Polyps on pinnules mostly 5–7 mm in transverse diameter, with four to five polyps per 3 cm.

Taxonomic remarks Despite molecular evidence suggesting a close relationship between *Alternatipathes maribilis* and *Alternatipathes venusta*, differentiating them underwater is challenging. The sole distinguishing feature - height of skeletal spines - is not visible using remotely operated vehicles (ROVs) or drop-down cameras. *A. maribilis*' polypar spines are small, measuring less than 0.01 mm, while *A. venusta*

possesses polypar spines exceeding 0.2 mm. This microscopic difference makes in situ identification challenging, confounding our understanding of their range extents.

Distribution Northeast Pacific Ocean (2,000–3,000 m); IOT (3,850 m).

Ecology and life history Many black coral species can be differentiated based on the type of ornamentation on their spines. For example, species in the family Antipathidae can be smooth, or possess different tubercle shapes and sizes. However, species in most genera of the family Schizopathidae lack ornamented spine surfaces (i.e., have smooth spines). This makes separating species more difficult and presents an interesting evolutionary history question; why do some lineages demonstrate increasing complexity of features on skeletal spines while others do not. Also, what is the function of spine ornamentation?

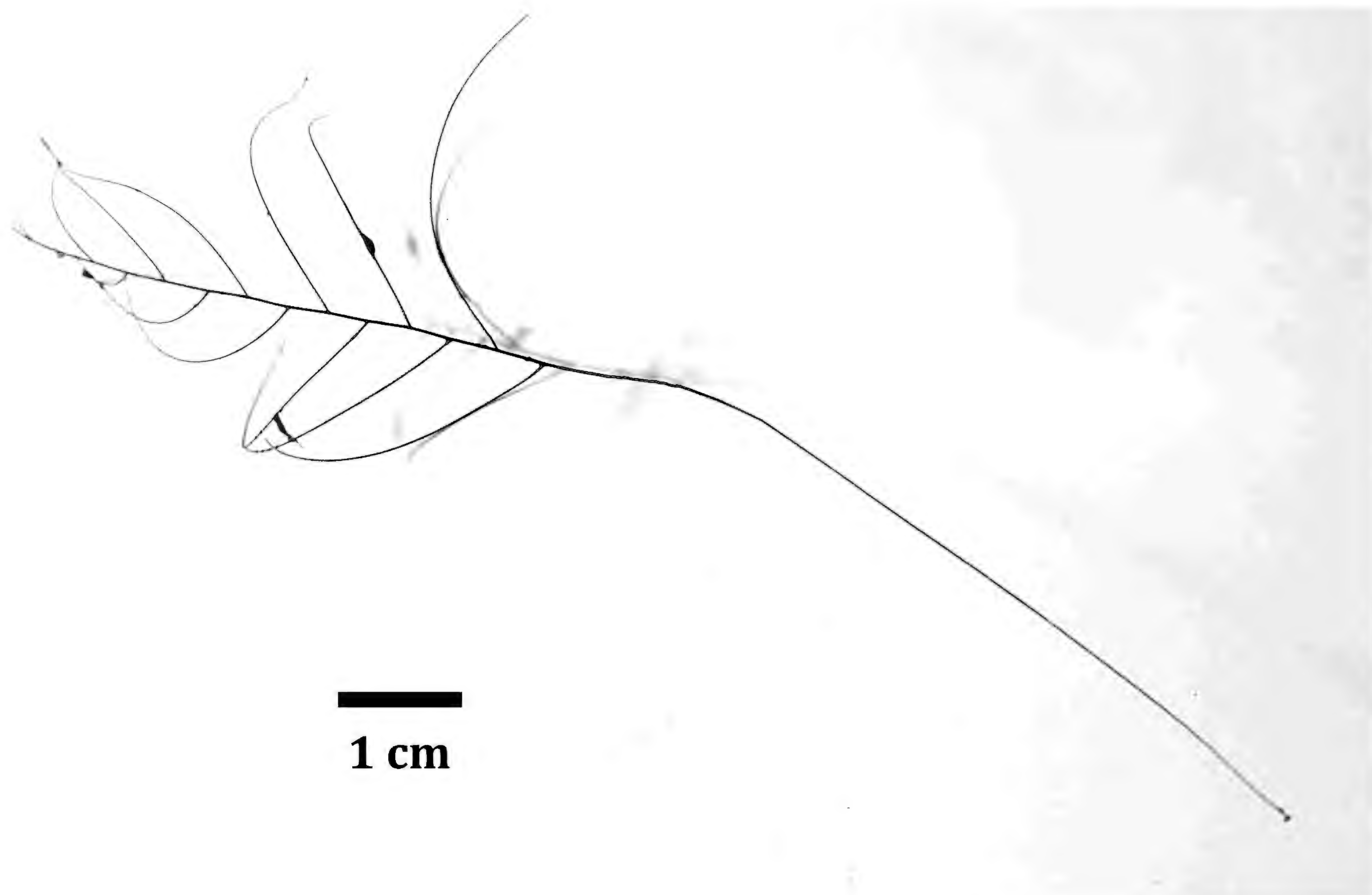
Alternatipathes venusta Opresko & Wagner, 2020

Figure 14. *Alternatipathes venusta*. (A) NMV F308485 (Op 120). (A) complete collected fragment.

Description of IOT material Colony attached, monopodial, unbranched, and pinnulate. Pinnules simple, arranged alternately in two lateral rows along upper part of stem. Lower unpinnulated section of the stem up to two times longer than upper pinnulated section. Pinnules generally decreasing in length proximally (>13 cm) to distally (3 cm) in a colony with a 17 cm long pinnulated section. Pinnules 4–6 mm apart on either side of axis; nine to 11 pinnules (total for both rows) per 3 cm. Polypar spines on pinnules, conical, smooth, acute, and up to 0.22 mm tall; a few are bifurcated. Abpolypar spines short, triangular, up

to 0.08 mm tall. Five to six rows of spines visible in lateral view; with 4 spines per mm within each row on polypar side; 3–4 spines per mm on abpolypar side. Polyps about 5 mm in transverse diameter, with 2 polyps per cm.

Taxonomic remarks See *Alternatipathes maribilis*: taxonomic remarks.

Distribution Northeast Pacific (2,000–3,000 m); IOT (3,854–5,000 m).

Ecology and life history See *Alternatipathes maribilis*: Ecology and life history.

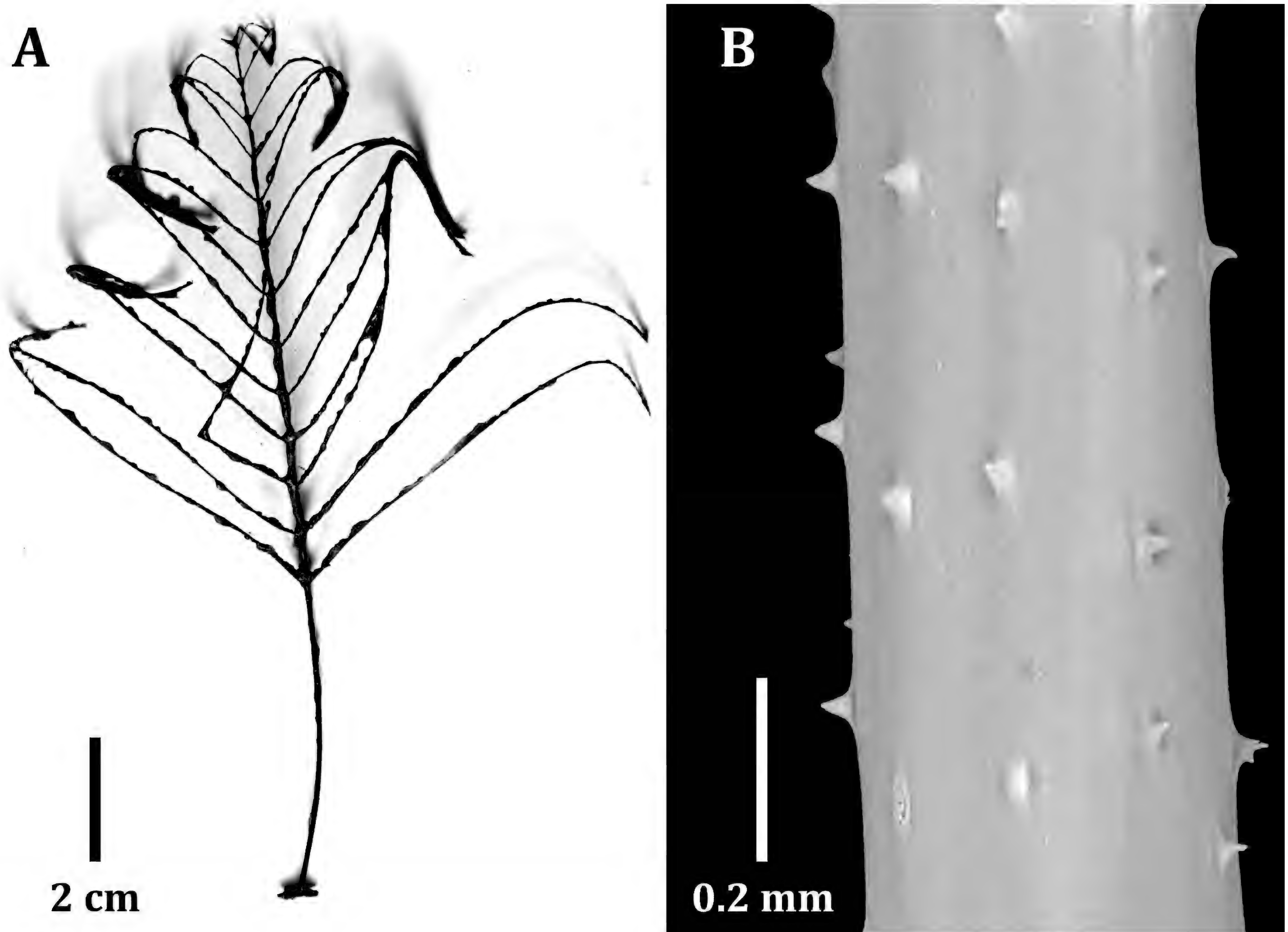
Bathypathes sp. Brook, 1889

Figure 15. *Bathypathes* sp. (A–B) NMV F308513 (Op 163). (A) complete collected fragment. (B) Section of skeleton showing spines.

Description of IOT material Corallum attached to substrate; monopodial, unbranched or rarely with a branch forming where the corallum has been broken and is regenerating. Pinnules simple, arranged alternately or suboppositely in two anterolateral or lateral rows. Length of pinnules on stem and branches usually longest near the middle of the pinnulated section of the corallum. Striatum present or absent. Spines conical, smooth, simple, forked or multiply knobbed at apex, with acute to slightly rounded apex. Spines often larger on polypar side of axis than on abpolypar side. Polyps from 2 mm to as much as 17 mm in transverse diameter.

Taxonomic remarks This IOT specimen has morphological characteristics most similar to *Bathypathes* by having no secondary pinnulation; however, the pinnules are arranged almost oppositely, which suggests it could be related to *Stauropathes*. Numerous specimens from different oceans with simple and nearly opposite pinnulation patterns have been collected, like the IOT specimen. These specimens might belong to an undescribed species; however, molecular data

of the IOT specimen to compare with these other specimens is required to determine if it too belongs to this potential new species.

Distribution Indian, Pacific, Atlantic, and Antarctic Oceans (800–4,000 m); IOT (510–3,100 m).

Ecology and life history Recent molecular studies on *Bathypathes* have revealed a disparity in depth distribution among nominal species ((Horowitz *et al.*, 2023b); (Quattrini *et al.*, 2023)). The existence of relatively shallow (< 1,000 m) and deep-sea (> 1,000 m) lineages within *Bathypathes* suggests that the two lineages belong to different genera or even families. Convergent evolution presents a compelling explanation for the observed morphological similarities despite potential genetic divergence. Furthermore, the observed depth zonation strongly suggests that depth acts as a key driver of speciation within *Bathypathes*, potentially leading to the ecological and evolutionary isolation of shallow and deep-sea populations. However, more molecular data are required before this taxonomic decision can be made.

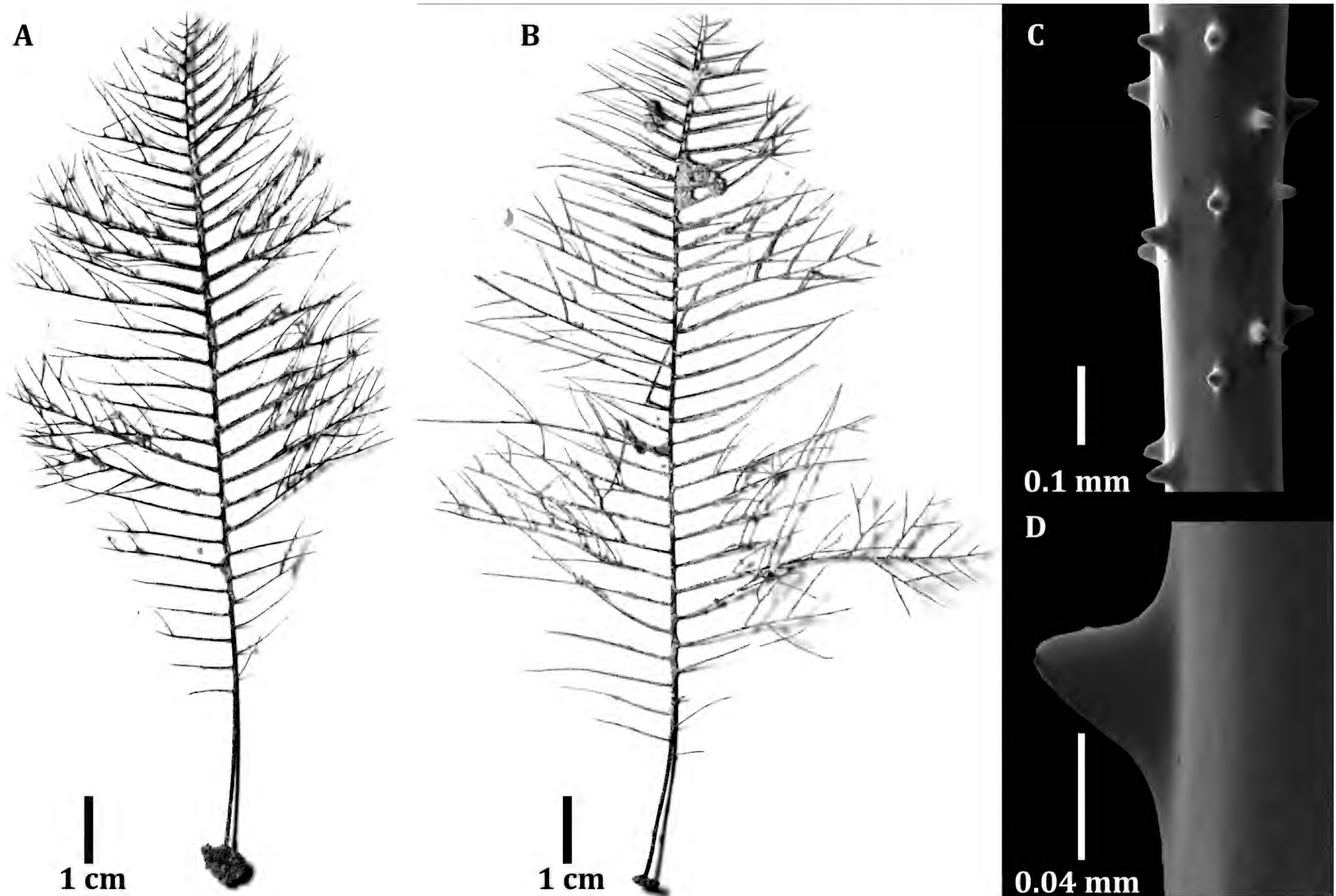
Lillipathes aff. *ventalina* Opresko, 2023

Figure 16. *Lillipathes* aff. *ventalina*. (A) NMV F308506 (Op 161). (A) complete collected fragment. (B–D) NMV F308509 (Op 161). (B) Section of two highest order branches. (C) section of skeleton showing spines. (D) Section of skeleton showing smooth spine surface.

Description of IOT material Corallum monopodial, flabellate, branched mostly to the second order, and pinnulate. Primary pinnules in four rows, two lateral and two anterolateral, and in alternating groups consisting of one lateral and one anterolateral pinnule on each side; the anterolateral pinnule in each pair usually positioned slightly below (proximal to) the lateral pinnule. Anterolateral pinnules projecting out of one side of the corallum. Pinnular density 10–14 per centimetre (total for both sides of the axis). Polypar spines up to 0.065 mm tall. Polyp density ranging from 2.5 to 3 per centimetre.

Taxonomic remarks *Lilipathpathes ventalina* was described from just one specimen shortly before the publication of this catalogue (Opresko, 2023). It is unclear how much intraspecific variation exists for

its defining characters. The main differences between these specimens and the holotype are the shape of the spines (IOT specimens rounder spine tips than the type) and the presence of anteriorlateral pinnules (only present along the top half of the pinnulated section of stem for IOT specimens compared to present along the entire pinnulated section of stem in the type). It is possible that the IOT specimens are younger than the type, further supported by the shorter total colony lengths compared to the holotype. More specimens and sequencing data are necessary to determine if the IOT specimens are a new species.

Distribution SouthWest Pacific Ocean (840–850 m); IOT (800 m).

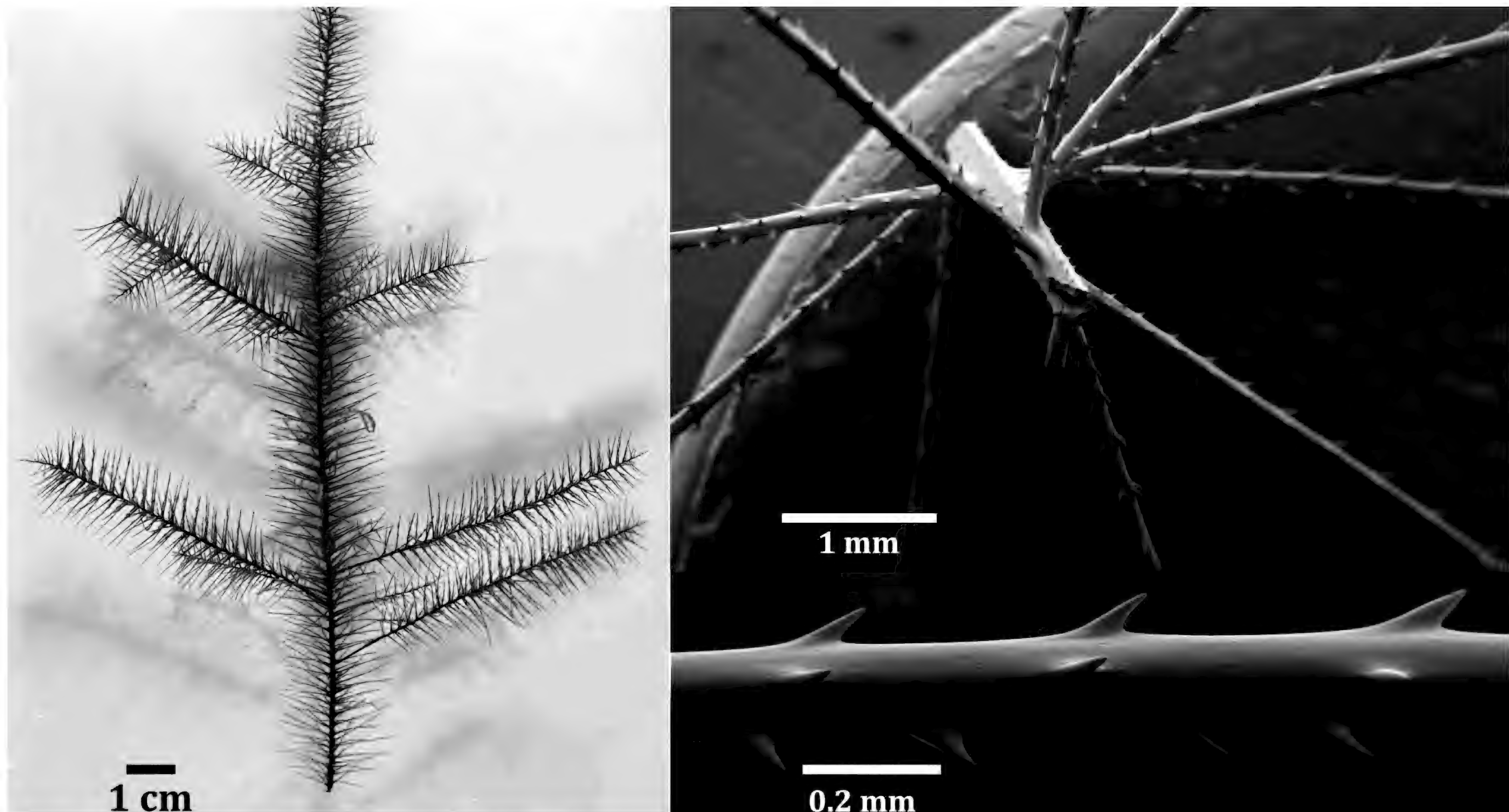
Parantipathes sp. Brook, 1889

Figure 17. *Parantipathes* sp.. (A–C) NMV F308500 (Op 176). (A) complete collected fragment. B. section of branch with pinnules. (C) section of pinnule showing spines.

Description of IOT material Corallum unbranched or sparsely branched; stem and branches pinnulate; pinnules simple, arranged biserially in 3 to 12 rows, and alternating in semi-spiral groups on opposite sides of stem or branch. Spines simple, smooth, distally directed or extend out in right angles to the axis. Polyps small, transversely elongate, and face towards distal end stem or branch.

Taxonomic remarks Species within the genus *Parantipathes* are differentiated based on metric relating to pinnule length, pinnule rows, and arrangement of pinnules per semispiral group Opresko (2015). However, there are many overlapping characters between species in this genus, and many species have yet to be sequenced to molecularly support morphological boundaries between species. Additionally, *Parantipathes* is polyphyletic, phylogenetically spread out across much of the Schizopathidae clade. Species from the North Pacific could represent a different genus

than the Atlantic *Parantipathes* - additional molecular investigations are required to review and revise the genus.

Distribution 66° N to 66° S (300–1,500 m); IOT (367–1400 m).

Ecology and life history Genera in the Schizopathidae are polyphyletic; however, resolving *Parantipathes*, along with *Lillipathes* and *Dendrobathypathes*, is taxonomically challenging based on mitochondrial DNA, because even though these three distinct genera appear different physically, their entire mitochondrial genomes show very little variation (Bledsoe-Becerra *et al.*, 2022). This lack of variation makes it difficult to tell the species apart using mitochondrial DNA and next generation sequencing techniques like genome skimming are required to resolve the taxonomy of this family.

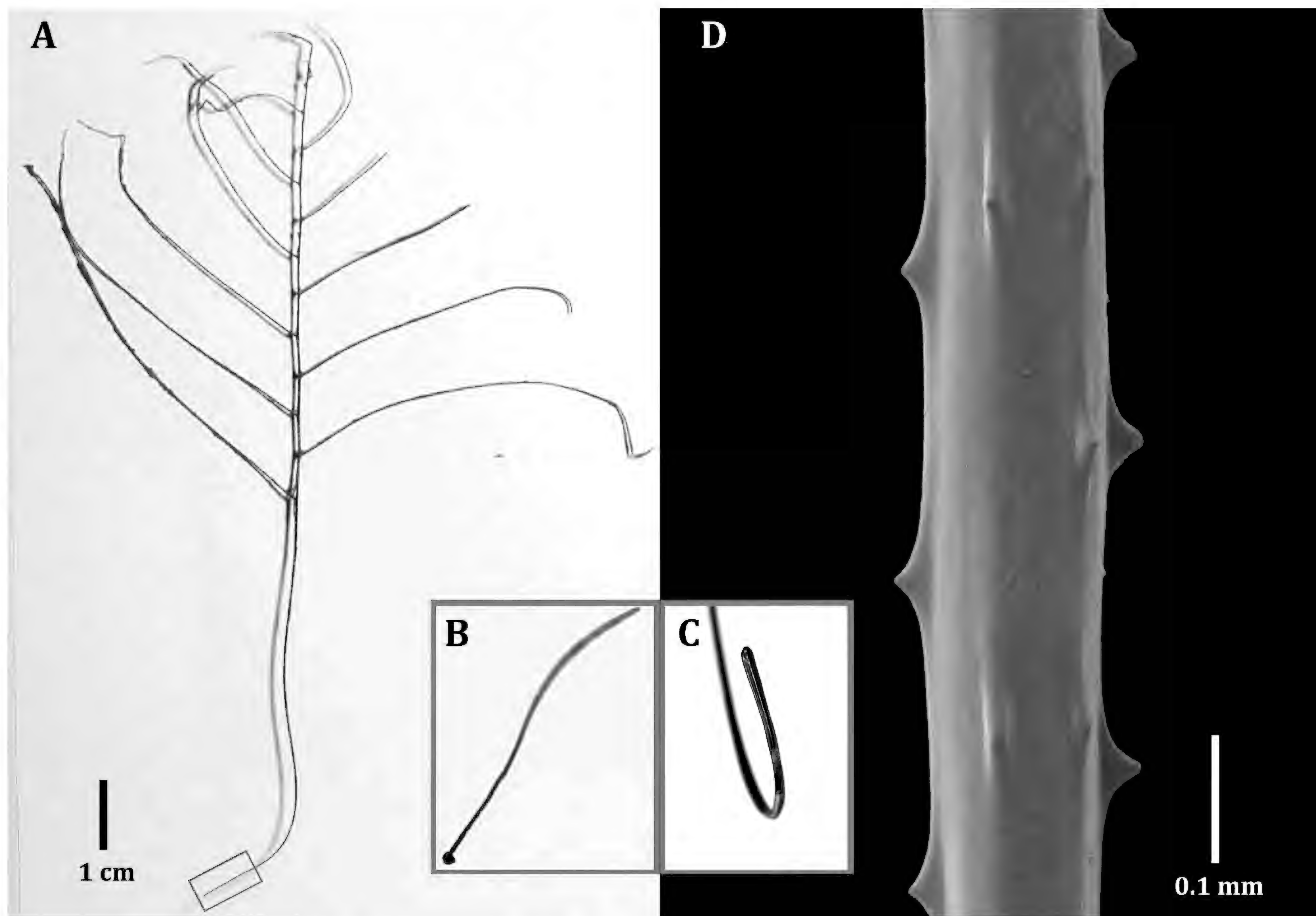
Schizopathes affinis Brook, 1889

Figure 18. *Schizopathes affinis*. (A-B) NMV F308502 (Op 122). (A) complete collected fragment. (B) Basal section of stem showing basal plate outlined in blue showing location on subfigure A. *Schizopathes affinis* (C) NMV F308511 (Op 122) Basal section of stem lacking basal plate. *Schizopathes affinis* (D) NMV F308502 (Op 122) section of skeleton showing spines.

Description of IOT material Colony monopodial, unbranched, pinnulate. Pinnules simple, arranged alternately in two lateral rows along stem; decreasing in length toward apex of corallum and inclined distally. Pinnules 8 mm to 10 mm apart proximally, 5 mm to 6 mm apart near the top of corallum (approximately seven pinnules total per 3 cm on lower part of corallum and about ten per 3 cm on upper part in holotype). Polypar spines small, triangular, and compressed; mostly 0.03 mm to 0.05 mm tall (up to 0.08 mm near distal end of pinnules); four to five rows visible in lateral view; with about six spines per mm. Abpolypar spines usually smaller than polypar spines, about 0.03 mm or absent. Polyyps 3 mm to 4.5 mm in transverse diameter, with about three polyyps per cm. .

Taxonomic remarks It is commonly thought that *Schizopathes* species are different than all other black corals by having a basal hook to grow in soft sediment while other genera have a basal plate to attach to hard

substrate. However, numerous IOT specimens had extremely tiny and fragile basal plates. It is possible that *Schizopathes* species also possess basal plates that are frequently detached during collection.

Distribution Pacific, Atlantic, and Antarctic Oceans (1,000–5,000 m); IOT (5,000 m).

Ecology and life history *Schizopathes affinis* represents a species in a lineage that has evolved unique morphological features to invade and persist in the abyss (Horowitz *et al.*, 2023b). This adaptation is the presence of a hooked proximal end of their stems to root into soft substrate. There are numerous, independent invasions into abyssal depths within the order, all within the last 50 million years (Horowitz *et al.*, 2023b). It is likely that anoxia in the abyss is the reason why there are no species from older lineages of black corals currently living in the abyss.

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Species index

Abyssopathes anomalia, 6
Abyssopathes lyra , 7
Abyssopathes lyraformis, 8
Alternatipathes alternata, 13
Alternatipathes maribilis, 14
Alternatipathes venusta, 15
Antipathes polyhedra, 3
Antipathes aff. *leptocrada*, 4
Aphanostichopathes sp., 5
Bathypathes sp., 16
Hexapathes bikofskii, 9
Hexapathes sp., 10
Leiopathes sp., 11
Lillipathes aff. *ventalina*, 17
Myriopathes sp., 12
Parantipathes sp., 18
Schizopathes affinis, 19

Species index

Abyssopathes anomalia, 6
Abyssopathes lyra , 7
Abyssopathes lyraformis, 8
Alternatipathes alternata, 13
Alternatipathes maribilis, 14
Alternatipathes venusta, 15
Antipathes polyhedra, 3
Antipathes aff. *leptocrada*, 4
Aphanostichopathes sp., 5
Bathypathes sp., 16
Hexapathes bikofskii, 9
Hexapathes sp., 10
Leiopathes sp., 11
Lillipathes aff. *ventalina*, 17
Myriopathes sp., 12
Parantipathes sp., 18
Schizopathes affinis, 19

Appendix - Antipatharia from voyages IN2021_V04 and IN2022_V08 to the Australian Christmas Island and Cocos (Keeling) Islands Territories

Family	Species	Operation	Accession no.	Specimen no.	Registration no.*
Antipathidae	<i>Antipathes leptocrada</i>	IN2022_V08 128	101	1	NMV F308523
Antipathidae	<i>Antipathes leptocrada</i>	IN2022_V08 128	102	20	NMV F308522
Antipathidae	<i>Antipathes leptocrada</i>	IN2022_V08 128	107	1	NMV F308525
Antipathidae	<i>Antipathes leptocrada</i>	IN2022_V08 128	108	2	NMV F308521
Antipathidae	<i>Antipathes leptocrada</i>	IN2022_V08 128	109	1	NMV F308518
Antipathidae	<i>Antipathes polyhedra</i>	IN2022_V08 179	102	1	NMV F308495
Antipathidae	<i>Antipathes polyhedra</i>	IN2022_V08 179	180	1	NMV F308587
Aphanipathidae	<i>Aphanostichopathes</i> sp.	IN2022_V08 108	154	1	NMV F308516
Aphanipathidae	<i>Aphanostichopathes</i> sp.	IN2022_V08 120	107	1	NMV F308488
Aphanipathidae	<i>Aphanostichopathes</i> sp.	IN2022_V08 122	108	1	NMV F308461
Aphanipathidae	<i>Aphanostichopathes</i> sp.	IN2022_V08 122	133	1	NMV F308445
Aphanipathidae	<i>Aphanostichopathes</i> sp.	IN2022_V08 122	136	1	NMV F308479
Aphanipathidae	<i>Aphanostichopathes</i> sp.	IN2022_V08 122	149	1	NMV F308441
Aphanipathidae	<i>Aphanostichopathes</i> sp.	IN2022_V08 122	150	1	NMV F308453
Aphanipathidae	<i>Aphanostichopathes</i> sp.	IN2022_V08 122	152	1	NMV F308448
Aphanipathidae	<i>Aphanostichopathes</i> sp.	IN2022_V08 128	112	1	NMV F308520
Aphanipathidae	<i>Aphanostichopathes</i> sp.	IN2022_V08 138	111	1	NMV F308493
Aphanipathidae	<i>Aphanostichopathes</i> sp.	IN2022_V08 161	103	1	NMV F308527
Aphanipathidae	<i>Aphanostichopathes</i> sp.	IN2022_V08 176	103	1	NMV F301498
Aphanipathidae	<i>Asteriopathes</i> sp.	IN2021_V04 009	102	1	MTQ G79988
Cladopathidae	<i>Abyssopathes anomala</i>	IN2022_V08 122	102	1	NMV F308451
Cladopathidae	<i>Abyssopathes anomala</i>	IN2022_V08 122	115	1	NMV F308466
Cladopathidae	<i>Abyssopathes anomala</i>	IN2022_V08 122	119	1	NMV F308440
Cladopathidae	<i>Abyssopathes anomala</i>	IN2022_V08 122	131	1	NMV F308478
Cladopathidae	<i>Abyssopathes anomala</i>	IN2022_V08 122	138	1	NMV F308447
Cladopathidae	<i>Abyssopathes anomala</i>	IN2022_V08 122	202	1	NMV F308472
Cladopathidae	<i>Abyssopathes anomala</i>	IN2022_V08 183	101	1	NMV F308489
Cladopathidae	<i>Abyssopathes anomala</i>	IN2022_V08 183	103	1	NMV F308491
Cladopathidae	<i>Abyssopathes lyra</i>	IN2022_V08 122	101	1	NMV F301497
Cladopathidae	<i>Abyssopathes lyra</i>	IN2022_V08 122	104	1	NMV F301496
Cladopathidae	<i>Abyssopathes lyra</i>	IN2022_V08 122	113	1	NMV F308465
Cladopathidae	<i>Abyssopathes lyra</i>	IN2022_V08 122	116	1	NMV F308508
Cladopathidae	<i>Abyssopathes lyra</i>	IN2022_V08 122	117	1	NMV F308458
Cladopathidae	<i>Abyssopathes lyra</i>	IN2022_V08 122	118	1	NMV F308464
Cladopathidae	<i>Abyssopathes lyra</i>	IN2022_V08 122	121	1	NMV F308450
Cladopathidae	<i>Abyssopathes lyra</i>	IN2022_V08 122	123	1	NMV F308439
Cladopathidae	<i>Abyssopathes lyra</i>	IN2022_V08 122	125	1	NMV F308470
Cladopathidae	<i>Abyssopathes lyra</i>	IN2022_V08 122	128	1	NMV F308452
Cladopathidae	<i>Abyssopathes lyra</i>	IN2022_V08 122	134	1	NMV F308460
Cladopathidae	<i>Abyssopathes lyra</i>	IN2022_V08 122	139	1	NMV F308474
Cladopathidae	<i>Abyssopathes lyra</i>	IN2022_V08 122	141	1	NMV F308601
Cladopathidae	<i>Abyssopathes lyra</i>	IN2022_V08 122	142	1	NMV F308473
Cladopathidae	<i>Abyssopathes lyra</i>	IN2022_V08 122	153	1	NMV F308446
Cladopathidae	<i>Abyssopathes lyra</i>	IN2022_V08 122	154	1	NMV F308449
Cladopathidae	<i>Abyssopathes lyra</i>	IN2022_V08 122	155	1	NMV F308442
Cladopathidae	<i>Abyssopathes lyra</i>	IN2022_V08 122	168	1	NMV F308443
Cladopathidae	<i>Abyssopathes lyra</i>	IN2022_V08 122	173	1	NMV F308462
Cladopathidae	<i>Abyssopathes lyra</i>	IN2022_V08 122	181	1	NMV F308456
Cladopathidae	<i>Abyssopathes lyra</i>	IN2022_V08 122	182	1	NMV F308438
Cladopathidae	<i>Abyssopathes lyra</i>	IN2022_V08 122	190	1	NMV F308599
Cladopathidae	<i>Abyssopathes lyra</i>	IN2022_V08 122	204	1	NMV F301495
Cladopathidae	<i>Abyssopathes lyra</i>	IN2022_V08 183	102	1	NMV F308492

Family	Species	Operation	Accession no.	Specimen no.	Registration no.*
Cladopathidae	<i>Abyssopathes lyra</i>	IN2022_V08 191	115	2	NMV F308585
Cladopathidae	<i>Abyssopathes lyriformis</i>	IN2022_V08 122	106	1	NMV F308603
Cladopathidae	<i>Abyssopathes lyriformis</i>	IN2022_V08 122	109	1	NMV F308501
Cladopathidae	<i>Abyssopathes lyriformis</i>	IN2022_V08 122	110	1	NMV F308598
Cladopathidae	<i>Abyssopathes lyriformis</i>	IN2022_V08 122	111	1	NMV F308444
Cladopathidae	<i>Abyssopathes lyriformis</i>	IN2022_V08 122	112	1	NMV F308469
Cladopathidae	<i>Abyssopathes lyriformis</i>	IN2022_V08 122	114	1	NMV F308597
Cladopathidae	<i>Abyssopathes lyriformis</i>	IN2022_V08 122	120	1	NMV F308475
Cladopathidae	<i>Abyssopathes lyriformis</i>	IN2022_V08 122	122	1	NMV F308457
Cladopathidae	<i>Abyssopathes lyriformis</i>	IN2022_V08 122	124	1	NMV F308468
Cladopathidae	<i>Abyssopathes lyriformis</i>	IN2022_V08 122	132	1	NMV F308600
Cladopathidae	<i>Abyssopathes lyriformis</i>	IN2022_V08 122	135	1	NMV F308454
Cladopathidae	<i>Abyssopathes lyriformis</i>	IN2022_V08 122	140	1	NMV F308467
Cladopathidae	<i>Abyssopathes lyriformis</i>	IN2022_V08 122	143	1	NMV F308455
Cladopathidae	<i>Abyssopathes lyriformis</i>	IN2022_V08 122	144	1	NMV F308463
Cladopathidae	<i>Abyssopathes lyriformis</i>	IN2022_V08 122	166	1	NMV F308471
Cladopathidae	<i>Abyssopathes lyriformis</i>	IN2022_V08 122	167	1	NMV F308437
Cladopathidae	<i>Abyssopathes</i> sp.	IN2022_V08 122	105	1	NMV F308596
Cladopathidae	<i>Abyssopathes</i> sp.	IN2022_V08 122	210	1	NMV F301494
Cladopathidae	<i>Abyssopathes</i> sp.	IN2022_V08 122	216	1	NMV F308602
Cladopathidae	<i>Abyssopathes</i> sp.	IN2022_V08 126	161	1	NMV F308494
Cladopathidae	<i>Hexapathes alis</i>	IN2022_V08 163	103	1	NMV F308504
Cladopathidae	<i>Hexapathes bikofskii</i>	IN2022_V08 163	101	1	NMV F308503
Cladopathidae	<i>Trissopathes</i> cf. <i>tetracrada</i>	IN2021_V08 048	101	1	MTQ G79993
Leiopathidae	<i>Leiopathes</i> sp.	IN2022_V08 128	103	1	NMV F308499
Leiopathidae	<i>Leiopathes</i> sp.	IN2022_V08 128	114	1	NMV F301499
Leiopathidae	<i>Leiopathes</i> sp.	IN2022_V08 128	122	1	NMV F308595
Leiopathidae	<i>Leiopathes</i> sp.	IN2022_V08 134	101	1	NMV F308524
Schizopathidae	<i>Alternatipathes alternata</i>	IN2022_V08 122	127	1	NMV F308480
Schizopathidae	<i>Alternatipathes alternata</i>	IN2022_V08 122	130	1	NMV F308459
Schizopathidae	<i>Alternatipathes alternata</i>	IN2022_V08 122	137	1	NMV F308477
Schizopathidae	<i>Alternatipathes alternata</i>	IN2022_V08 122	146	1	NMV F308481
Schizopathidae	<i>Alternatipathes mirabilis</i>	IN2022_V08 120	101	1	NMV F308484
Schizopathidae	<i>Alternatipathes mirabilis</i>	IN2022_V08 120	103	1	NMV F308487
Schizopathidae	<i>Alternatipathes mirabilis</i>	IN2022_V08 120	110	1	NMV F308486
Schizopathidae	<i>Alternatipathes mirabilis</i>	IN2022_V08 120	141	1	NMV F308483
Schizopathidae	<i>Alternatipathes</i> sp.	IN2022_V08 106	107	1	NMV F308594
Schizopathidae	<i>Alternatipathes</i> sp.	IN2022_V08 120	156	1	NMV F301493
Schizopathidae	<i>Alternatipathes</i> sp.	IN2022_V08 120	163	1	NMV F301492
Schizopathidae	<i>Alternatipathes</i> sp.	IN2022_V08 128	104	1	NMV F308510
Schizopathidae	<i>Alternatipathes</i> sp.	IN2022_V08 161	102	1	NMV F308496
Schizopathidae	<i>Alternatipathes</i> sp.	IN2022_V08 176	104	1	NMV F308498
Schizopathidae	<i>Alternatipathes</i> sp.	IN2022_V08 183	107	1	NMV F308490
Schizopathidae	<i>Alternatipathes venusta</i>	IN2022_V08 120	102	1	NMV F308482
Schizopathidae	<i>Alternatipathes venusta</i>	IN2022_V08 120	154	1	NMV F308485
Schizopathidae	<i>Alternatipathes venusta</i>	IN2022_V08 122	151	1	NMV F308507
Schizopathidae	<i>Bathypathes ptiloides</i>	IN2022_V08 151	101	1	NMV F308514
Schizopathidae	<i>Bathypathes ptiloides</i>	IN2022_V08 163	102	1	NMV F308513
Schizopathidae	<i>Bathypathes</i> sp.	IN2021_V04 046	101	1	MTQ G79992
Schizopathidae	<i>Lillipathes ventalina</i>	IN2022_V08 161	101	1	NMV F308509
Schizopathidae	<i>Lillipathes ventalina</i>	IN2022_V08 161	104	1	NMV F308506
Schizopathidae	<i>Parantipathes</i> sp.	IN2021_V04 018	103	1	MTQ G379990
Schizopathidae	<i>Parantipathes</i> sp.	IN2022_V08 111	101	1	NMV F308517
Schizopathidae	<i>Parantipathes</i> sp.	IN2022_V08 128	110	1	NMV F308526
Schizopathidae	<i>Parantipathes</i> sp.	IN2022_V08 128	113	1	NMV F308512
Schizopathidae	<i>Parantipathes</i> sp.	IN2022_V08 176	101	1	NMV F308500
Schizopathidae	<i>Parantipathes</i> sp.	IN2022_V08 176	102	1	NMV F308497
Schizopathidae	<i>Schizopathes affinis</i>	IN2021_V04 024	101	1	MTQ G79991

Family	Species	Operation	Accession no.	Specimen no.	Registration no.*
Schizopathidae	<i>Schizopathes affinis</i>	IN2022_V08 122	103	1	NMV F308511
Schizopathidae	<i>Schizopathes affinis</i>	IN2022_V08 122	107	1	NMV F308502
Schizopathidae	<i>Schizopathes affinis</i>	IN2022_V08 122	126	1	NMV F308519
Schizopathidae	<i>Schizopathes affinis</i>	IN2022_V08 122	129	1	NMV F308505
Stylopathidae	<i>Tylopathes</i> sp.	IN2021_V04 009	105	1	MTQ G79989
unknown	<i>Antipatharia</i> sp.	IN2022_V08 122	145	1	NMV F308476

* MTQ - Museum of Tropical Queensland, Townsville; NMV - Museums Victoria, Melbourne